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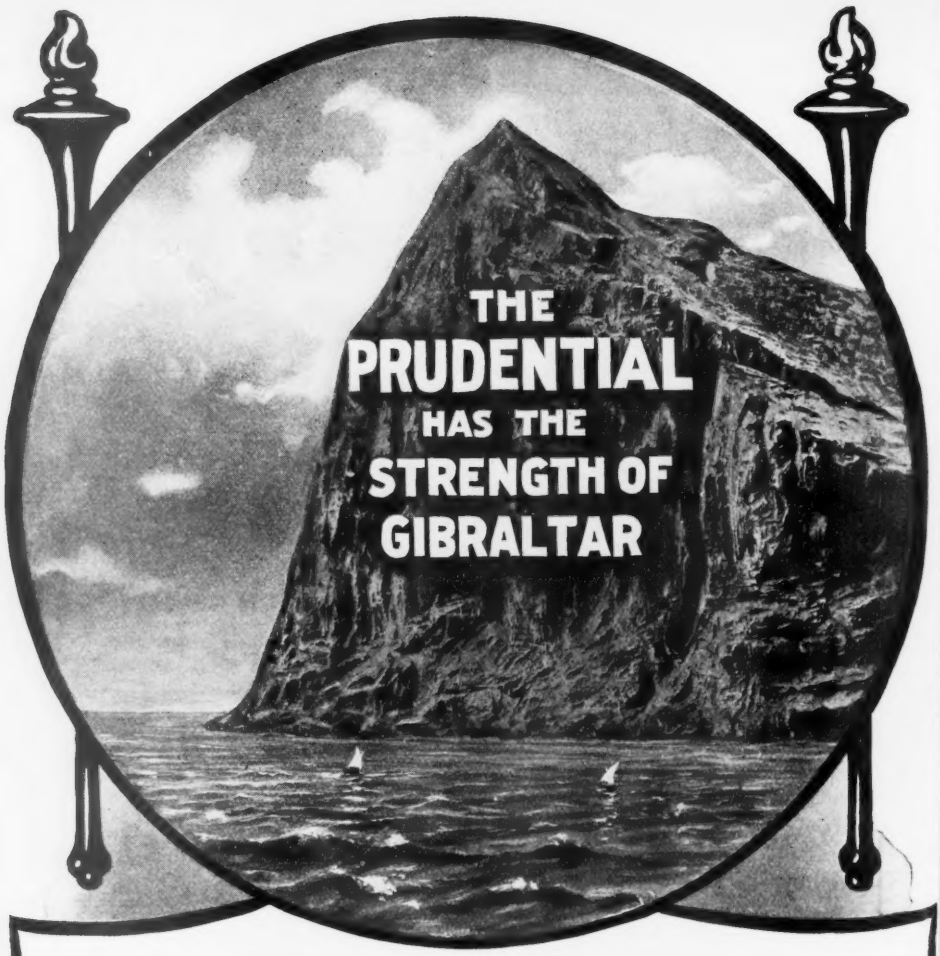

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VOLUME XXXVIII NUMBER 1

BOTANICAL GAZETTE

JULY, 1904

SPERMATOGENESIS AND OOGENESIS IN EPHEDRA TRIFURCA.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LIX.

W. J. G. LAND.

(WITH PLATES I–V)

THE Gnetales are exceedingly important from a morphological standpoint because of many points of contact with angiosperms. That they have not received the attention their character warrants is probably due to the difficulty encountered in obtaining material suitable for critical morphological study.

Ephedra, comprising about twenty species, is confined to the warmer arid regions of the northern hemisphere, and is evidently more nearly related to the Coniferales than is either Tumboa or Gnetum.

Important morphological literature dealing with Ephedra is extremely scanty. In 1872 Strasburger published an account of *Ephedra altissima* and *E. campylopoda*, dealing with the development of the microsporangiate and megasporangiate strobili. In 1879 he described stages in the development of the embryo in *E. altissima*. Jaccard ('94) described in a fragmentary way *E. helvetica*, giving most attention to spermatogenesis. He also gave some attention to fertilization and early stages of embryogeny.

The present study was undertaken with the hope of being able to follow in a fairly complete way the life-history of *E. trifurca* Torr. This account, dealing with spermatogenesis and oogenesis, is to be followed shortly by another dealing with fertilization and embryogeny.

METHODS.

Material was collected in the vicinity of Mesilla Park, N. M., from December 20, 1902, to May 11, 1903. The second collection was made one month after the first; and as development became more rapid collections were made at intervals of four days. The strobili, attached to a short piece of the stem, were packed in wet cotton, and on reaching the laboratory four days later were placed in a moist chamber to enable them to recover turgescence. That fixation immediately after removal from the tree is not absolutely necessary is shown by nuclei in all stages of division. Further treatment did not differ essentially from approved methods of microtechnique.

THE STAMINATE STROBILUS.

E. trifurca is monosporangiate, and the staminate as well as the ovulate strobili are borne in whorls around the nodes of the stem. Exceptional instances were noted in which the strobili were bisporangiate (*fig. 1*). Strasburger figures such a strobilus in *E. campylopoda*, and refers to it as an abnormal inflorescence. In another instance two ovules were present in a staminate strobilus of *E. trifurca*, although one is the usual number in the ovulate strobilus. This last, however, has many exceptions.

Shaw ('96) reports a strobilus of *Sequoia sempervirens* in which the upper part was ovulate and the lower staminate. Dickson ('60) observed the same thing in *Picea excelsa*. Coulter and Chamberlain ('01) figure strobili of Abies which are staminate at the apex and base and ovulate between. Goebel ('01) observed that in *Pinus maritima* the microsporangia were at the base of the strobilus and the megasporangia above. In the middle region he found rudimentary ovuliferous scales in the axils of the microsporophylls. In Tumboa the flowers are functionally monosporangiate, but in the center of a whorl of stamens there is a single functionless ovule with a spirally coiled micropyle. This seems to indicate that at a not remote period of its history the flowers were perfect. Ephedra, however, appears to have gone a step farther, and has become wholly monosporangiate; and the occasional bisporangiate strobili are reversions. It seems that, instead of regarding such occasional strobili as abnormal, it is better to consider them as atavistic; as pointing back to a bisporangiate

ancestry. Atavistic tendencies should not be lightly passed over, for it is from such reversions that we may expect valuable hints as to previous conditions.

THE MICROSPORANGIUM.

In the first material collected, December 20, 1902, the group of cells which gives rise to the staminate flower is shown in *fig. 2*. No archesporial cells are yet distinguishable either by size or staining reactions, nor is the beginning of the perianth visible. Cell division is proceeding quite rapidly, and there is apparently considerable activity throughout the winter months.

A month later the perianth is quite well developed (*fig. 3*). The cells immediately beneath the epidermis are about the same size as the adjacent ones, and as yet no differentiation into archesporium can be recognized. At the base of the strobili the flowers are much farther advanced than at the apical region. Later in the season all stages from rudimentary sporangia to mother-cells may be found in the same strobilus.

Fig. 4 shows a later stage in the development of an anther taken from the base of a strobilus. There is no positive evidence that the archesporium rises from a single hypodermal cell, but such is probably the case. The primary wall layer divides periclinally, giving rise to the wall layer and tapetum. The wall-cells do not divide periclinally, all divisions being anticlinal (*figs. 5, 6*). The sporogenous cells do not divide in any definite plane (*fig. 5*). The stages shown in *fig. 5* were common in basal sporangia February 9, 1903.

Fig. 6 shows a more advanced stage of the sporangium. The wall layer and tapetum are completely separated, and the sporogenous cells have ceased to divide; in fact, they are spore mother-cells which have not yet taken on the appearance which is characteristic of older mother-cells (February 15, 1903). A little later the wall-cells become flattened by the growth of the mother-cells and the tapetum. No further anticlinal division of the wall-cells takes place after they begin to be flattened. They become much stretched by the further growth of the adjacent cells. The tapetal cells increase in size and stain intensely, this last because of the presence of food in large quantities. *Fig. 7* shows a more advanced stage. The wall-cells are

beginning to disintegrate, the tapetal cells are increasing in size and dividing anticlinally, and the mother-cells are in the resting condition (February 15, 1903).

In gymnosperms the number of wall layers varies considerably. In Cycadales, Lang ('97) found the wall of Stangeria to consist of from three to six layers; in Ginkgoales they number from four to seven. Chamberlain ('98) found the wall of *Pinus Laricio* to be almost constantly three-layered. Coker ('02) found three wall layers in Podocarpus, the cell-walls of which are very thin and ultimately collapse; and in Taxodium he found a single layer. In *E. trifurca* the wall is a single layer of cells, and Strasburger found the same condition in the species studied by him.

In *E. trifurca* numerous instances were observed in which individual tapetal cells were not distinguishable from adjacent mother-cells. This seems to indicate that the tapetum is potentially sporogenous, and by virtue of its position has become sterile. With the appearance of the mother-cell the history of the sporophyte ends.

In general the resting stage of the microspore mother-cell in gymnosperms is long. Chamberlain ('98) observed mother-cells in *Pinus Laricio*, *Cupressus Lawsoniana*, and *Taxus baccata canadensis* in October. The reduction division occurred about May 1, thus giving a resting period of about seven months. In Ephedra the first observed reduction division was on March 12, giving a resting period of about one month.

At the time of the reduction division the cells of the wall layer are reduced to nuclei, scarcely a trace of cytoplasm being present. The cells of the tapetal layer become conspicuously vacuolated and their nuclei much enlarged. The nuclei become usually about four times the volume of those of the epidermal cells (*fig. 7*). Two or more nuclei are present in many tapetal cells at the time tetrads are formed. These last divisions appear to be amitotic, and nuclei in all stages, from the dumb-bell stage to complete separation, can be seen. At this time the tapetal cells, especially those nearest the bottom of the loculi, become enormously distended and very vacuolate (*fig. 14*). Soon afterwards they become a flattened plate and disappear.

THE REDUCTION DIVISION AND MALE GAMETOPHYTE.

As has been said, the microspore mother-cell remains in the resting stage about one month. The mother-cells up to the late prophase are filled with starch, which now quickly disappears. There does not at all times seem to be uniformity in the stages of division in the cells of a loculus. Instances were observed in which all the cells of a loculus were in the same phase of division. Again, those in the upper part of a loculus were in synapsis, those at the bottom had formed tetrads, while all intermediate stages were between.

The spirem segments into twelve chromosomes (not all of which are shown in *fig. 8*), which as they come to lie in the equatorial plane of the nucleus are short and thick, closely massed, and can be counted only with extreme difficulty. The result of repeated countings made in various stages of the first division, as well as in the second, leaves no doubt that the gametophyte number is twelve. Jaccard reports eight in *E. helvetica*.

Twelve appears to be the prevailing number of chromosomes in the gametophytes of gymnosperms. Three exceptions to this statement are to be noted: Overton ('93) reports eight for *Ceratozamia mexicana;* Strasburger ('04) finds eight in *Taxus baccata;* the other is *E. helvetica*, with eight according to Jaccard. Dixon ('98) reported eight chromosomes for *Pinus sylvestris*, but Blackman ('98) and Miss Ferguson ('01) have shown beyond doubt that the number in this species is also twelve.

Each chromosome apparently consists of four rods lying in extremely close contact. In the heterotypic division (*fig. 9*) the chromosome divides longitudinally, the ends opening out to form the X, Y, V, and O forms which are characteristic of the heterotypic division in higher plants. A membrane (*figs. 11, 12*) begins to form between the daughter-nuclei, as if spores of the bilateral type are to result, but in the great majority of cases the membrane wholly disappears, and the spores are of the tetrahedral type; although instances were noted in which they are probably bilateral. The second division in the pollen mother-cell is homotypic (*fig. 13*) and immediately follows the heterotypic division. In this second division longitudinal splitting of the chromosomes can be seen with little difficulty. The J form is quite conspicuous. As the chromosomes separate, in

many instances they become quite irregular, being stretched almost to the point of breaking. It is quite possible that irregular numbers of chromosomes, which are occasionally reported in plants, may have originated by the breaking of an individual chromosome. The microspores, still within the wall of the mother-cell, quickly assume an oval form (*fig. 14*).

After a brief period of rest (*fig. 15*) the nucleus of the microspore divides, and the first prothallial cell is formed. It has been determined beyond a reasonable doubt that a wall is laid down between the two nuclei (*figs. 16, 17*), although it is extremely difficult to differentiate. The prothallial cell is pressed closely against the end of the microspore by the growth of the other cell, its nucleus usually taking the meniscus form (*figs. 17–22*). The other cell, still remaining at the center of the spore, enlarges, and dividing (*fig. 17*) gives rise to the second prothallial cell and the antheridium initial (*fig. 18*). The antheridium initial does not appear to be separated from the second prothallial cell by a wall, but both nuclei remain in the same mass of cytoplasm which originally surrounded the nucleus before division (*fig. 18*). Here again arises a great difficulty in making conclusive observations. It may be that a wall is laid down and almost immediately resorbed, as Juel ('00) has shown to be the case in tetrad formation in *Carex acuta*, where a cell plate is formed and immediately resorbed, leaving the tetrad nuclei free within the wall of the mother-cell. It is conceivable that such a wall may be laid down, for it must be remembered that the entire prothallial region of gymnosperms is undergoing modification, in that the prothallial cells are either more or less ephemeral or altogether wanting; and that when cells are becoming obsolescent the wall is the first to disappear, leaving the two nuclei free within the common cytoplasm; next, the nucleus occasionally fails to divide; and finally no division takes place at all.

The second prothallial cell becomes flattened because of pressure due to the growth of the antheridium initial, and its nucleus becomes plano-convex or even meniscus-shaped, with its plane or concave face turned toward the first prothallial cell (*figs. 18, 20*). The nucleus of the antheridial cell, still at the center of the microspore, enlarges very much (*fig. 18*) and divides (*fig. 19*), giving rise to the generative

cell and the tube nucleus (*fig. 20*). The tube nucleus, although lying in close proximity to the wall of the microspore, does not become flattened as do the prothallial cells. In all preparations examined there seems to be no break in the cytoplasm surrounding the tube nucleus and the second prothallial cell (*figs. 20–22*), nor is a wall laid down between the tube nucleus and the primary spermatogenous cell. The primary spermatogenous cell—or generative cell—lies in a mass of cytoplasm differentiated from the surrounding cytoplasm by a slightly denser zone (*figs. 20, 21*). This condition of affairs is doubtless comparable to that of the generative cell of angiosperms, where there is a well-defined *Hautschicht*, on the outside of which food material is conspicuous. The primary spermatogenous cell dividing (*fig. 21*) gives rise to the stalk cell and the body cell, both of which lie within the cytoplasmic ring previously mentioned as surrounding the primary spermatogenous cell. The male gametophyte at this time (April 1, 1903) contains five nuclei: two prothallial cells, tube nucleus, stalk cell, and body cell. The microspore will be shed ten to fifteen days later.

The time periods in the development of the strobilus and male gametophyte are as follows: The strobilus appeared the previous season; on December 20, 1902, the group of cells which gives rise to the staminate flower is apparent, but the "perianth" is not yet visible; January 27, 1903, the "perianth" is well along and the primordia of the sporangia are clearly apparent; February 10, the primary wall cells are dividing; by February 15 many sporangia have mother-cells in the resting condition; one month later (March 15) the reduction division takes place; by April 1 the spores are mature, and about April 15 the pollen is shed. These records are for one season only, and the periods may be expected to vary somewhat in other seasons, the variations being of course dependent on various external factors.

It appears that Jaccard never saw the prothallial cells, for he says that at maturity the pollen grain contains three nuclei: "a large central nucleus representing the antheridial cell of Belajeff and of Strasburger; and two vegetative polar nuclei, of which one is the tube nucleus (*noyau du tube pollinique, Pollenschlauchkern*), and the other homologous with the *Stielzelle* of the German authors." So, putting this into present terminology, what he saw at the shedding of the pollen

were tube nucleus, stalk cell, and body cell. It is hardly to be expected that two prothallial cells will be present in one species and wholly absent in another.

The number of prothallial cells varies in gymnosperms. Those in which two have been reported are *Ginkgo*, Strasburger ('92); *Larix europaea*, Strasburger ('84); *Picea vulgaris*, Belajeff ('93); *Pinus Laricio*, Coulter and Chamberlain ('01); *Podocarpus coriacea*, Coker ('02); *Ceratozamia longifolia*, Juranyi ('82), sometimes two, but more often one. Those in which one has been reported are *Ceratozamia*, Juranyi ('82); *Zamia*, Webber ('97); *Cycas*, Ikeno ('98); *Ephedra campylopoda*, Strasburger ('72). No prothallial cells have been observed in *Biota*, *Cupressus*, and *Juniperus*, Strasburger ('92); *Taxus baccata*, *Juniperus*, Belajeff ('93); *Thuja occidentalis*, Land ('02); *Taxodium distichum*, Coker ('03); *Cupressus* (4 spp.), *Taxus baccata* and 4 vars., *Juniperus* (2 spp.), *Chamaecyparis* (5 spp.), *Callitris*, *Cryptomeria japonica*, and *Thuja orientalis*, Coker ('04); *Ephedra helvetica*, Jaccard ('94).

It is quite probable that in many gymnosperms two prothallial cells will be found eventually, and probably one at least will be found in some of those forms where up to the present none have been demonstrated.

THE OVULATE STROBILUS.

The ovulate strobilus was first collected in December. It differs in external appearance from the staminate strobilus in that it is longer and more slender.

The ovulate flower is not differentiated as early as is the staminate. On March 1, 1903, traces of the outer and inner integuments could be seen; a few days later the integuments presented the appearance shown in *fig. 23*. Much has been said concerning these integuments or perianths, as they are variously called. Transverse sections at different levels (*figs. 24, 25*) show that the outer integument results from a fusion of four leaves, and the inner integument from a fusion of two leaves. The outer integument becomes several cells thick, and in later stages quite hard. The inner integument is never more than two cells thick. A short time before the pollen is shed, the inner integument rapidly elongates and thrusts itself out through the apex of the strobilus. The exposed end is wide open, and is also

slit a short distance down one side (*fig. 44*). The pollen enters the open end of the integument, and drops down to the bottom of the pollen chamber (*fig. 44*), where it lies in contact with the archegonial end of the female gametophyte. So far as known, there is no other gymnosperm in which the pollen grain is placed so near the archegonia.

The archesporium could not be traced definitely back to a single hypodermal cell, but there are indications that such may be its origin. The earliest stage in which a suggestion of differentiation was observed is shown in *fig. 26*, March 8, 1903. The lower larger cell in this figure is beyond doubt the megaspore mother-cell. The large cell above will divide again and again, and thus place the megaspore mother-cell deeply within the nucellus. In *fig. 27* the divisions of a similar cell are clearly apparent, and the conspicuous megaspore mother-cell is shown. In general not more than one megaspore mother-cell is organized, but instances were noted in which two and very rarely three mother-cells were present. Sometimes, but not always, each of these cells produce megaspores. In general one mother-cell soon gains an advantage over the others and causes their rapid disintegration.

The mother-cell grows rapidly, meanwhile encroaching on the surrounding nucellar tissue. The reduction division occurred about March 8, 1903 (*fig. 28*). The second division quickly follows the first, and the more deeply placed megaspore alone functions. According to both Strasburger and Jaccard, three megaspores only are produced in the forms studied by them. In *E. trifurca* either three or four may occur (*figs. 29, 30*). In many instances the upper cell does not divide; again, the division may be incomplete, or it may be completed entirely. In no observed instance does the division of the upper cell take place until two lower megaspores are entirely separated; *fig. 29* shows such a late division of the upper cell. It seems that the more deeply placed cell because of its relation to the food supply is enabled to divide first. From this it follows that the most favorably placed megaspore—the lower one—is enabled to grow so rapidly as to preclude much further development on the part of the others. The megaspore remains a very short time in the resting condition. The number of chromosomes at the reduction division is

twelve, thus confirming the observations made on the microspore series.

Lang ('97) has shown that in Stangeria the mother-cell forms a row of three megaspores; Treub ('81) reports the same for Ceratozamia; and three are reported for Ginkgo. Among the Coniferales four are frequent. In *Pinus Laricio* I have observed that either three or four are formed indifferently. Strasburger ('79) gives three as the usual number in Taxus, although four frequently occur; in his later work on *Taxus baccata* (04') he says that four cells are formed from the megaspore mother-cell. Juel ('00) finds four in *Abies sibirica* and *Larix sibirica;* Shaw ('96) reports four in Sequoia; Lawson ('04) studying the same species of Sequoia finds three; Coker ('03) finds three in *Taxodium distichum* and ('04) four in *Thuja orientalis*, where they are not arranged in a row, but in nearly regular tetrad form. Strasburger finds three in *Ephedra campylopoda*, and Jaccard three in *E. helvetica;* in *E. trijurca* three or four are formed indifferently, dependent on the rapidity with which the functioning megaspore encroaches. This encroachment is probably the reason for the differences reported in the forms mentioned above.

THE FEMALE GAMETOPHYTE.

The two nuclei resulting from the division of the megaspore seem invariably to take the position with reference to the major axis of the ovule shown in *fig. 31*, for in no observed instance did the nuclear plate vary from this position. Before the spindle fibers and cell-plate have disappeared, a ring-like vacuole appears, entirely surrounding the cell-plate. The rapid increase in size of this vacuole is one of the chief factors concerned in the parietal placing of the free nuclei. These two nuclei divide simultaneously, and the resulting four take equidistant positions at the periphery of the embryo sac (*fig. 32*). Successive simultaneous divisions (*figs. 33, 35*) rapidly follow each other until the maximum number of nuclei is reached, which in the present instance apparently does not exceed 256. It may be of interest to note that at only one time—immediately after the division of the megaspore—is the vacuole free from cytoplasm. Careful staining shows that at all later stages (*figs. 32–35*) it is filled with a delicate cytoplasmic structure, which gradually increases in density until free nuclear division ceases, which was about April 1,

1903. Free nuclear division, therefore, extends through a period of approximately twenty days.

Simultaneously with the appearance of walls, the gametophyte is differentiated into two distinct regions: a micropylar or sex-organ producing region, and an antipodal or nutritive region. The behavior of the lower part of the gametophyte is strongly suggestive of the same region in *Gnetum Gnemon*, as described by Lotsy ('99). The cells of the antipodal region are only slightly elongated and are fairly regular in outline. As growth proceeds—and it is very rapid—this lower part is again separated into two physiologically distinct regions: storage and haustorial. The storage region comprises the greater part of the gametophyte, and is highly charged with starch and other foods. In the center are a few rows of thin-walled cells containing much more food than the surrounding cells, and extending up to the base of the archegonia. It is down through this thin-walled region that the embryo is thrust by the elongation of the suspensor. The haustorial part of the gametophyte (*fig. 44*) is composed of one or two layers of the outermost cells, which are clearly haustorial in function. Those at the tip of the gametophyte are elongated to a point ending in a single cell. The haustorial cells do not have the great elongation shown by the cells in the same region of Zamia. The storage and haustorial region increases in size as long as the embryo continues to grow.

The region in the immediate vicinity of the archegonia and for some distance below is very loosely organized, and the cell-walls are extremely delicate. In the central region immediately beneath the archegonia instances were noted in which the walls were late in appearing. The cells of this region are very vacuolate, and in consequence have little contents.

This feebly organized region is significant from a phylogenetic standpoint. In Tumboa the upper part of the gametophyte is loosely organized, and the numerous cells which function as eggs never get beyond the archegonium initial stage. In *Gnetum Gnemon* the same region never gets beyond the free nuclear stage, and these free nuclei function directly as eggs. It is possible that Ephedra, Tumboa, and Gnetum show stages through which the ancestral forms of angiosperms in all probability passed.

THE ARCHEGONIUM.

About April 1, 1903, the archegonium initials were first observed. They are the pyramidal form common to most gymnosperms. Two is the usual number, one is occasional, and three are rare. The primary neck-cell is quickly cut off after the initial becomes apparent (*fig. 36*), and almost immediately divides periclinally (*fig. 37*). Other periclinal walls follow (*fig. 40*), sometimes as many as four or five tiers being cut off before anticlinal walls appear; and as many as eight tiers of neck cells have been observed. Each tier divides anticlinally into four cells; later there may be six or eight in a tier, also the walls which come in later are no longer truly periclinal, thus giving the neck a somewhat irregular appearance (*fig. 41*). Thirty-two is probably the minimum number of cells, but it may go much higher. *Fig. 39* shows a cross section of the neck 40 μ above the top of the central cell. Of all gymnosperms Ephedra has the longest-necked archegonium. This may be due to the fact that the archegonial end of the gametophyte is freely exposed to the air.

Simultaneously with the appearance of the archegonium initials, a change is observable in the nucellus. Traces of disorganization become visible at the tip of the nucellus and gradually proceed downward, so that by the time the ventral nucleus is cut off, the cells at the apex of the nucellus have completely disappeared, leaving a pollen-chamber shaped like the frustrum of an inverted cone. The pollen-grains are thus enabled to come in direct contact with the gametophyte and the necks of the archegonia. So far as has been reported, Ephedra is the only gymnosperm having any part of the gametophyte exposed freely to the air, except in the case of *Cycas circinalis*, where, according to Warming ('77), if fertilization does not occur, the gametophyte continues to grow, ultimately bursting out through the micropyle and developing chlorophyll on exposure to light. Strasburger's figures show a pollen-chamber in *E. altissima*, but not in *E. campylopoda;* and Jaccard finds one present in *E. helvetica*. In Cycadales and Ginkgoales the pollen-chamber, formed by disintegration of the cells of the nucellar beak, is a conspicuous feature. In *Pinus Laricio* it is so small as to escape notice in most instances, while in *Thuja occidentalis* the tip of the nucellus at the time of pollination is an expanded stigma-like surface.

The nucleus of the central cell lies in close proximity to the neck of the archegonium. As the central cell enlarges, it does not have a conspicuous vacuole in the center, like Pinus and the Cupressineae, but is almost completely filled with cytoplasm except in the immediate vicinity of the nucleus, where there are a few small vacuoles. Later the cytoplasm in the lower part of the archegonium becomes almost homogeneous. A conspicuous kinoplasmic mass lies at a little distance below the nucleus (*fig. 41*). In the earliest stages it is coarsely granular, and later becomes dense, and is larger and sharper in outline than the similar body which is so conspicuous in some of the pines and in *Thuja occidentalis*.

G.S.L.

When two or three archegonia are present, one is usually smaller than the others, as is shown in *fig. 38* (a cross-section through the middle region of the archegonia). When one archegonium is present it is very large as compared with the larger of two in a gametophyte. It is questionable if the eggs in the smaller archegonia regularly function.

The jacket-cells are at first rectangular, with the longer axis at right angles to the long axis of the central cell (*fig. 40*). Since periclinal division does not keep pace with the elongation of the central cell, the jacket-cells become much elongated (*fig. 41*). Their walls, never at any time thick, become so tenuous that they can scarcely be seen, and evidently offer little resistance to the passage of food into the central cell. There is evidence that at the time of fertilization the walls separating them from the egg break down altogether. *Fig. 41* shows two archegonia at the time of pollination (April 15, 1903).

The ventral nucleus was cut off about April 15 in the season of 1903. In material collected during the season of 1904 from the same plants, the ventral nucleus was cut off about April 1. This difference is probably due to the fact that the season of 1904 was unprecedentedly hot and dry.

No trace of a wall can be seen between the ventral nucleus and the egg, although in some instances there is a suggestion of cytoplasmic thickening between the two nuclei. The cytoplasm at the upper end of the central cell is still quite vacuolate; in the lower part it has now become very dense, in fact almost homogeneous.

The ventral nucleus remains in the upper part of the archegonium, and enlarging (*fig. 42*) becomes very conspicuous. The egg nucleus passes to the center of the archegonium, enlarges, and surrounds itself with a mass of cytoplasm, slightly different from that farther away from the nucleus in that it at first consists of radial strands proceeding out from the nucleus in all directions. A thickening of the cytoplasm next appears all around the nucleus at the place where the radiations meet the general cytoplasm of the archegonium. This thickening is very pronounced in most instances, again it can be seen with difficulty; it very much resembles the first appearance of the membrane around the egg and synergids of angiosperms.

SUMMARY.

Ephedra trifurca is monosporangiate, but bisporangiate strobili occasionally occur.

The beginnings of the staminate flower were clearly apparent in December, and the pollen was shed about the middle of April, the interval being thus a little over four months.

The anthers develop in acropetal succession on a strobilus, and are surrounded by a perianth.

Microspore mother-cells were observed about the middle of February, and the reduction division occurs about one month later.

The gametophyte number of chromosomes is twelve.

There are two persistent prothallial cells; the first is cut off by a wall; the second is not cut off by a wall.

The primary spermatogenous cell surrounds itself by a membrane (*Hautschicht?*), and on the division of the primary spermatogenous cell, the stalk cell and body cell continue to be surrounded by this membrane, and are not separated from each other by a wall.

The only wall formed in the pollen grain is the one which cuts off the first prothallial cell.

The male gametophyte at the time of shedding consists of two prothallial cells, stalk cell, body cell, and tube nucleus.

The megasporangium is surrounded by two integuments, the outer of which consists of four fused leaves; the inner of two fused leaves.

The megaspore mother-cell is deeply placed within the nucellus

and gives rise to either three or four megaspores arranged in a row, the most deeply placed megaspore being functional.

The nuclei resulting from the division of the megaspore show polarity in that they are definitely oriented with respect to the axis of the megasporangium.

A vacuole appears between the nuclei resulting from the division of the megaspore before the spindle has disappeared, and soon becomes filled with delicate cytoplasmic structures which increase in density until walls appear.

The free nuclei are parietally placed from the beginning, divide simultaneously, and are presumably 256 in number before walls appear.

The female gametophyte is separated into two regions: a loosely formed archegonial region, and a more compact antipodal region, the latter being composed of a haustorial and a storage region.

The archegonia vary from one to three, two being the usual number; the neck is composed usually of eight tiers of cells; and there are no archegonial chambers.

The apex of the nucellus breaks down, and a conspicuous pollen-chamber is formed. The necks of the archegonia are thus exposed to the air, and the microspores are brought directly into contact with the female gametophyte.

No wall is formed between the ventral nucleus and the egg; the former becomes quite large and takes a position a short distance below the neck of the archegonium.

The egg takes a position midway in the cytoplasm of the archegonium, surrounds itself with a membrane comparable to the one which invests the eggs of angiosperms, and in this position awaits fertilization.

At the time of fertilization the cytoplasm in the archegonium has become almost homogeneous and very dense, except in the region immediately below the neck of the archegonium, where it is loosely vacuolate.

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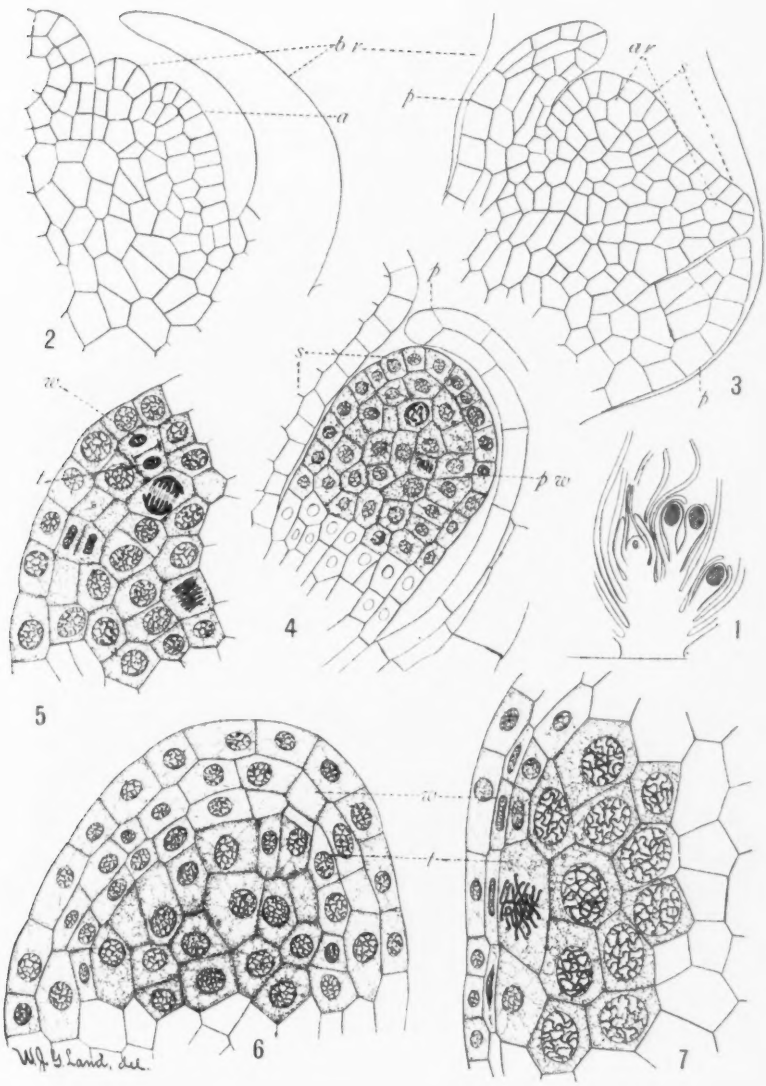

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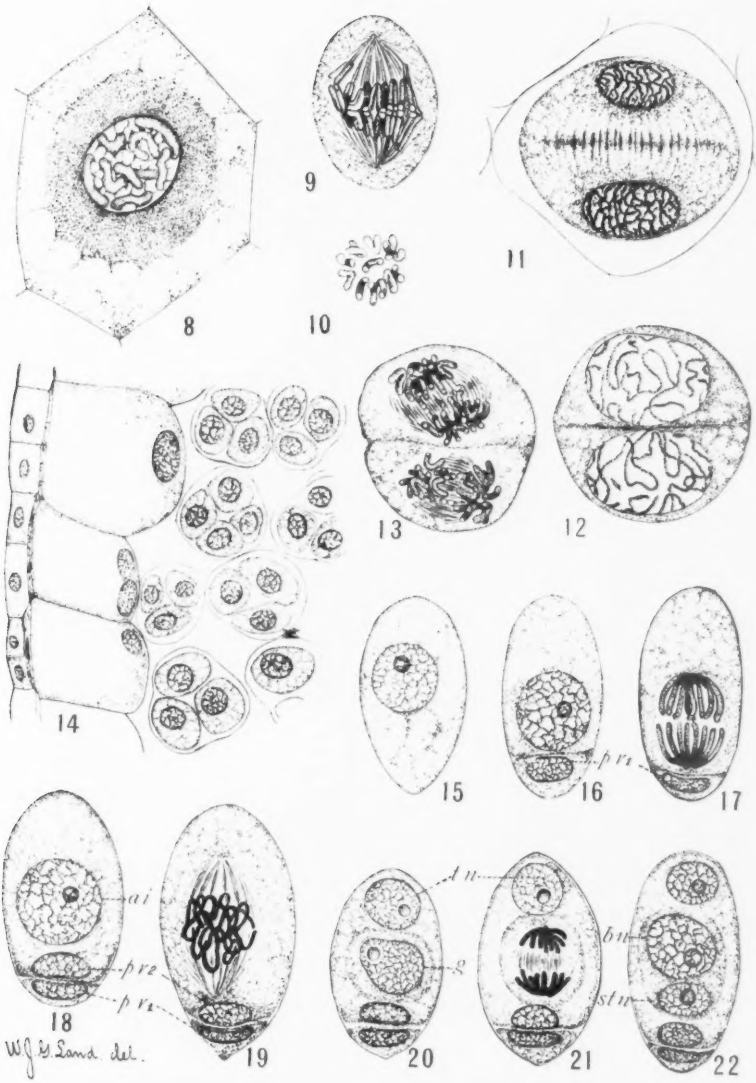

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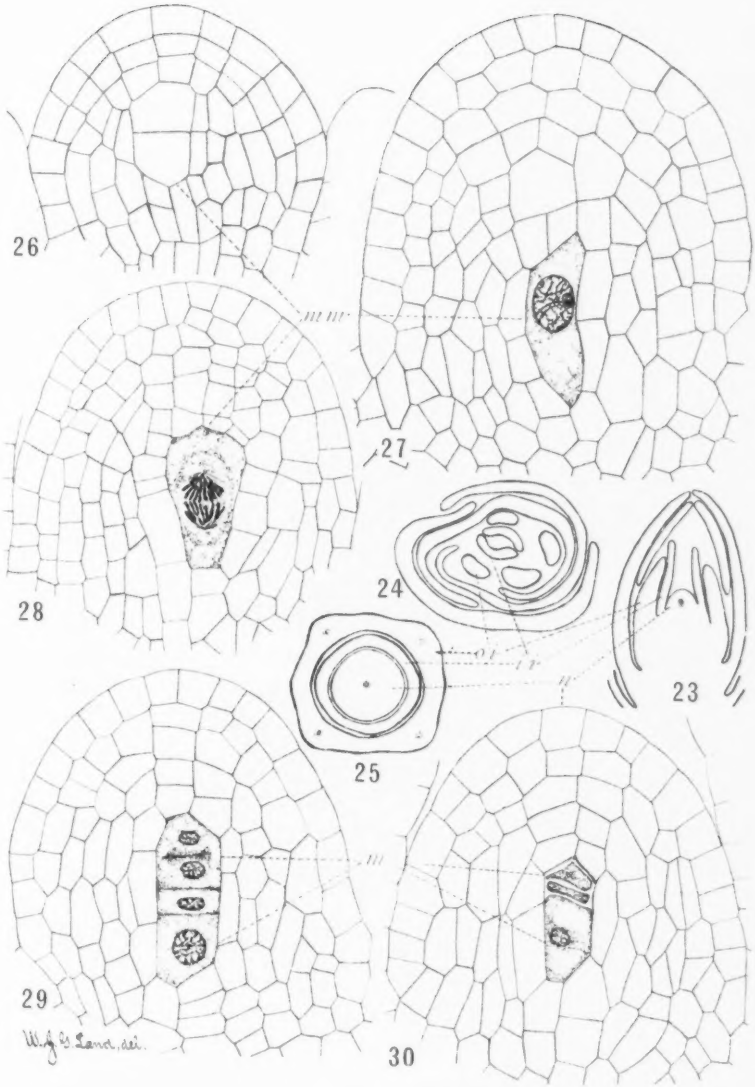

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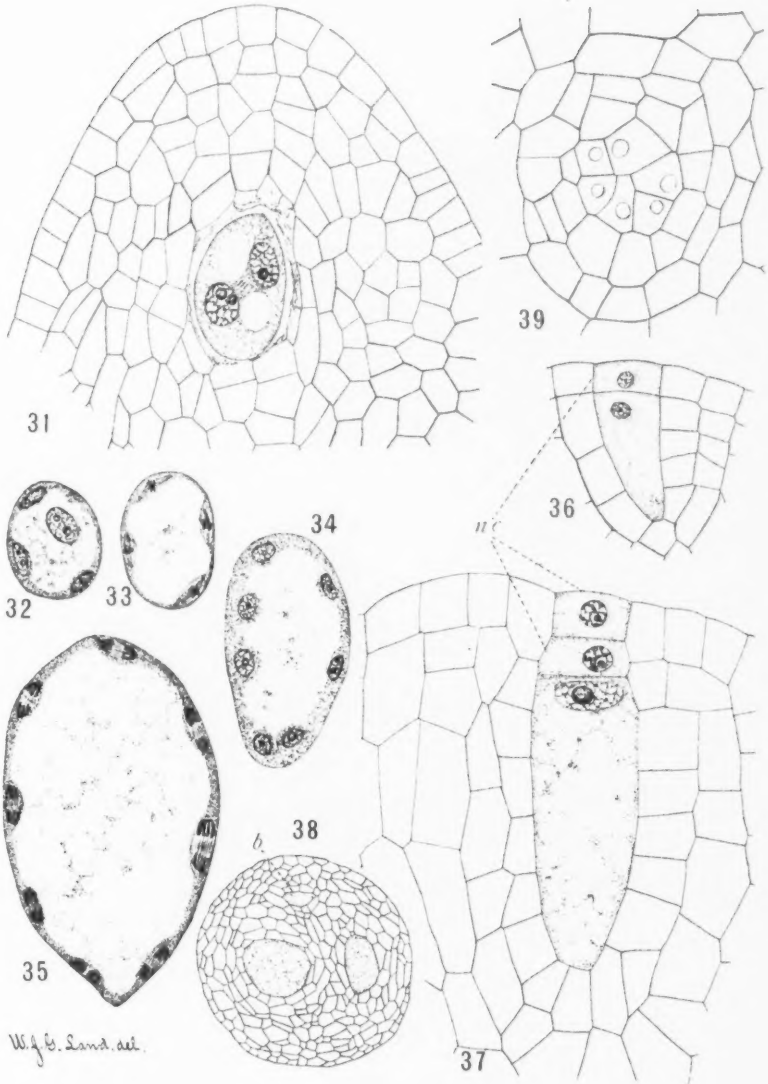

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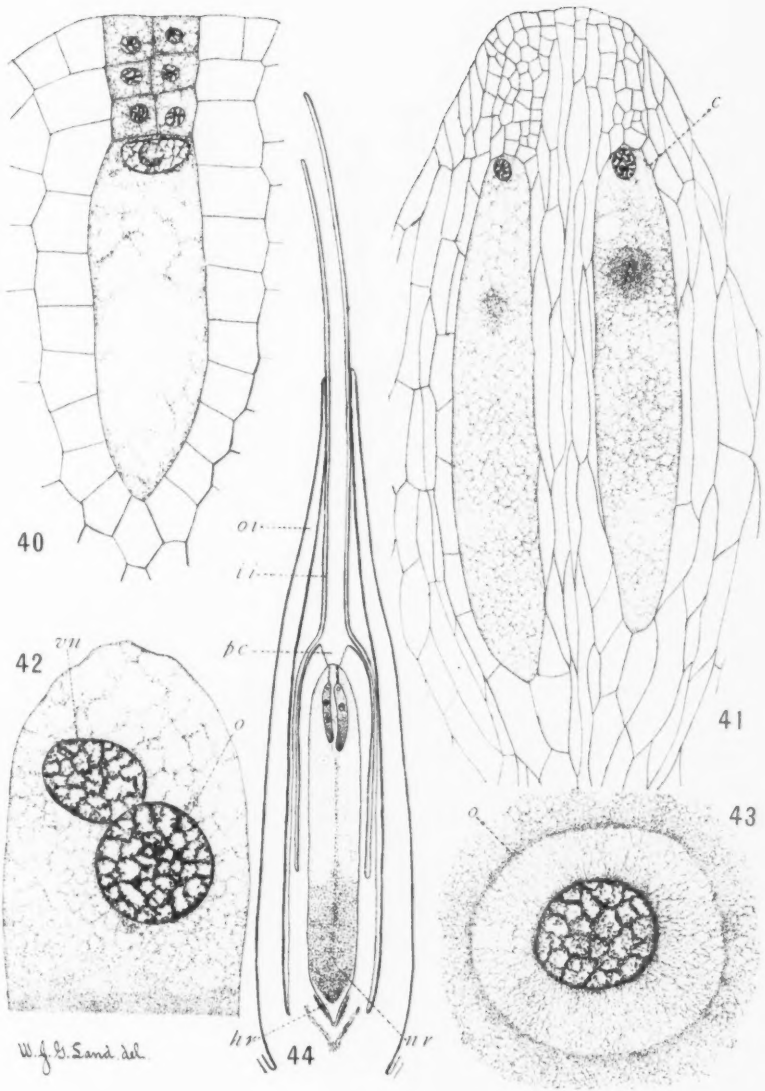

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EXPLANATION OF PLATES I–V.

All figures were drawn with an Abbé camera lucida, and reduced one-half in reproduction. Abbreviations are: *br*, bract; *a*, primordium of stamen; *p*, perianth; *oi*, outer integument; *ii*, inner integument; *n*, nucellus; *pc*, pollen-chamber; *s*, microsporangium; *pw*, primary wall-cells; *w*, wall-cells; *t*, tapetum; *ar*, archesporial cells; *pr*^{1}, first prothallial cell; *pr*^{2}, second prothallial cell; *ai*, antheridium initial; *tn*, tube nucleus; *g*, primary spermatogenous cell; *stn*, nucleus of stalk cell; *bn*, nucleus of body cell; *mm*, megaspore mother-cell; *m*, megaspores; *nr*, nutritive region of female gametophyte; *hr*, haustorial region of gametophyte; *b*, abortive archegonium; *nc*, neck cells; *c*, central cell; *vn*, ventral nucleus; *o*, egg.

FIG. 1. A bisporangiate strobilus. × 16.

FIG. 2. Portion of a longitudinal section through a staminate strobilus showing bracts and primordia of two anthers. × 225.

FIG. 3. Longitudinal section through an anther showing beginning of perianth and primordia of two sporangia. × 225.

FIG. 4. Longitudinal section through a sporangium showing sporogenous cells, part of an adjoining sporangium, and perianth × 225.

FIG. 5. Division of primary wall cells; the sporogenous cells are also actively dividing. × 500.

FIG. 6. Early stage of the microspore mother-cells. × 500.

FIG. 7. Microspore mother-cells in resting stage. × 500.

FIG. 8. Microspore mother-cell after segmentation of the spirem. × 1500.

FIG. 9. Microspore mother-cell, heterotypic division. × 1500.

FIG. 10. Polar view of chromosomes in anaphase of second mitosis in microspore mother-cell. × 1500.

FIG. 11. Later stage in division of microspore mother-cell. × 1500.

FIG. 12. Prophase of homotypic division. × 1500.

FIG. 13. Homotypic division. × 1500.

FIG. 14. Tetrads and enlarged tapetal cells. × 500.

FIG. 15. A microspore shortly before the first division. × 1500.

FIG. 16. Microspore after formation of first prothallial cell. × 1500.

FIG. 17. Division to form second prothallial cell and antheridium initial. × 1500.

FIG. 18. First and second prothallial cells and antheridium initial. × 1500.

FIG. 19. Division of antheridium initial. × 1500.

FIG. 20. Two prothallial cells, primary spermatogenous cell, and tube nucleus. × 1500.

FIG. 21. Division of primary spermatogenous cell. × 1500.

FIG. 22. The two prothallial cells, stalk cell, body cell, and tube nucleus. × 1500.

FIG. 23. Median longitudinal section through a megasporangiate strobilus showing the two integuments and nucellus with gametophyte. × 46.

FIG. 24. Section through the strobilus above the nucellus showing the four parts of the outer integument and the two parts of the inner integument which later become tubes. × 46.

FIG. 25. Section through the strobilus at level of gametophyte, showing the fused parts. × 46.

FIG. 26. Megaspore mother-cell becoming differentiated. × 500.

FIG. 27. Megaspore mother-cell, resting stage. × 500.

FIG. 28. Megaspore mother-cell dividing. × 500.

FIG. 29. A row of four megaspores, showing late division of upper daughter nucleus. × 500.

FIG. 30. A row of three megaspores; the upper daughter-nucleus has failed to divide. × 500.

FIG. 31. First division of the megaspore, showing formation of the central vacuole. × 500.

FIG. 32. Four-celled stage of female gametophyte. × 500.

FIG. 33. Simultaneous division of the nuclei; eight-celled stage. × 500.

FIG. 34. Female gametophyte; sixteen cells. × 500.

FIG. 35. Female gametophyte; simultaneous division to form sixty-four free nuclei. × 500.

FIG. 36. Archegonium with primary neck cell and central cell. × 500.

FIG. 37. Archegonium showing the enlarged central cell and two neck cells. × 500.

FIG. 38. Transverse section of gametophyte at level of central cell, showing a large, a small, and an abortive archegonium. × 75.

FIG. 39. Transverse section through neck of an archegonium at a distance of 40 μ above the central cell. × 500.

FIG. 40. An archegonium slightly older than *fig.* 37. × 500.

FIG. 41. Two archegonia just before the division of the nucleus of the central cell. × 112.

FIG. 42. Egg nucleus and ventral nucleus lying in the upper part of the archegonium. × 500.

FIG. 43. Egg lying near the center of archegonium and surrounded by a membrane of thickened cytoplasm, and ready for fertilization. × 500.

FIG. 44. Longitudinal median section through the ovule and integuments, showing reproductive, storage, and haustorial regions of the gametophyte × 48.

THE WATER-RELATION OF PUCCINIA ASPARAGI.

A CONTRIBUTION TO THE BIOLOGY OF A PARASITIC FUNGUS.

RALPH E. SMITH.

(WITH TWENTY-ONE FIGURES)

WHETHER the use of the term "ecology" would be consistent and proper throughout the present article, the writer must confess his inability to decide. With plants of independent existence ecology has become a well-defined branch of botanical science, but when complicated with the phenomena of parasitism there must be distinguished two fairly distinct classes of life-relations; those which act upon the parasitic organism directly, and those which affect it, even more decidedly perhaps, in a secondary or indirect manner through their effects upon the host-plant. "Biology," in the European sense, seems on the whole a more fitting term for the present purpose; since at many points it is difficult to say whether we are considering the relation of the parasite to its environment, or to its host's environment, or whether its host is its environment. The subject is one of ecology in the broadest sense, yet a distinction must be made between the relations of an organism to natural influences, and its relations to the effects of perhaps the same influences upon another organism upon which it lives as a parasite. The fungus has no soil-relation, of course, but its connection with the host-plant is much more than this, though corresponding to a certain extent. Without extended discussion on this point, it will suffice to say that it has seemed to the writer very desirable to establish upon a systematic basis the relations existing between parasitic fungi in general and the various influences exerted upon them in nature, either directly or acting through the medium of the host-plant. While many scattered observations of this kind exist, very little definite work has been done in establishing general principles or in drawing definite conclusions. The observations contained herein are offered as a modest contribution in this direction.

It is well established in a general way that the development of

those fungi that live upon higher plants is favored by wet weather. This is so universally the case that we may almost conclude without further consideration that under normal conditions the water-relation of such parasites is of more importance in their development than any

FIG. 1.—Asparagus rust, *Puccinia Asparagi* DC., in all stages. Milpitas, Calif., July 4, 1903.

other condition. Considering this as established, there still remains a broad field for research in determining just why this is true, and in general in analyzing the conditions and their results. This has been the writer's object in the case of the destructive parasite *Puccinia Asparagi* DC., which has proved especially favorable for such study.

The asparagus rust is caused by one of the Uredineae of the subdivision *Auleupuccinia* of Schroeter's classification; that is, the spermogonia, aecidia, uredospores, and teleutospores all develop upon the same plant. This is shown in *fig. 1*, where the various spore forms may be readily recognized. Upon the stalks represented at the extreme right and left all four forms are present at once. This disease has long been known in Europe, but attained no prominence in this country until the fall of 1896, since which time it has spread entirely across the continent from Massachusetts to California, with extremely disastrous results to the asparagus industry.

The development of this rust is practically the same as that of others of the same class, the spermogonia and aecidia appearing in spring, followed by the uredo stage in summer, after which the teleuto or black rust appears. The development of the aecidial stage has varied, according to the writer's observation, with the nature of the spring climate in various sections of the country. In Massachusetts, where the spring is comparatively late and short, the aecidium of *Puccinia Asparagi* is not unknown, but is by no means common, and the development of this stage of the rust is decidedly limited. Going south to Long Island and New Jersey, the spring form is common, but by no means noticeable; while in California the "spring rust" is almost as well known to asparagus-growers as the later stages, and upon old beds, volunteer growth, or beds too young for cutting, it reaches a development quite unknown in the east, sometimes covering the main stalk and branches of the plant completely and causing considerable damage. *Fig. 2* illustrates a case of

FIG. 2.—Aecidial development of the rust as seen in California. Bouldin Island, April 29, 1903.

this sort. The uredo and teleuto stages follow in order as the season progresses, and while the simultaneous occurrence of these forms is by no means unknown, it is usual, as with most similar rusts, for the uredo stage to develop almost exclusively during the summer, when the plants are most active, followed by a pure teleuto growth upon the dead stalks in fall. The latter stage in all the Eupuccinia group is regarded, therefore, as typically the fall rust, and as a form which develops to any extent only in the latter part of the season as a result of the approach of winter and the death of the host-plant.

The relation of the development of the asparagus rust to soil and atmospheric moisture has received some attention in previous publications. Stone and Smith[1] found a decided difference in the prevalence of the disease according to the moisture-retaining properties of the soil, the trouble being worse upon the drier soils. So marked was this difference in Massachusetts that in regions equally exposed to infection, and in fact equally affected with the teleuto stage in the fall, the beds upon heavier, moist soils did not show, and have never shown, any rust previous to September (when the plants mature in that climate); while those upon light dry soils became badly affected with the uredo stage early in the season. The difference not only appeared in different sections of the state in the same season, but also in the whole state in different seasons, the amount of rust in the most affected localities varying as the season was wet or dry, being least in the wet seasons. Although not universally accepted at first, this idea has received much support from subsequent experience over practically the whole country.

In most of the large asparagus regions of the eastern states but little difference exists between the soils of the various plantations, the characteristic soil being of a light, sandy, dry nature. In the first violent epidemic of the rust everything was affected in such sections, and differences in soil, as well as in varieties of asparagus and other factors now recognized by all, were overlooked or imperceptible. A tour of these districts at present, however, will convince the most skeptical that of the original beds those few which now remain are almost entirely upon the heavier soils, and of the new beds the most

[1] Bulletin 61, and Ann. Reports 12, 14, 15, Hatch Exper. Station of Mass. Agric. College.

thrifty are likewise on the heavier soils, other things being even approximately equal. Most of the growers in the large eastern asparagus districts recognize this, and likewise attribute the marked freedom from rust of the past two seasons to the very unusual rainfall, which fact is in itself strong evidence of the unfavorable effect of abundant soil moisture upon the fungus.

This is, of course, contrary to the established principle above mentioned that such parasites are greatly favored by wet seasons. One of the most prominent features in the observations of Stone and Smith was the occurrence in the asparagus beds least affected of the teleuto stage alone coming on at the usual time, but not preceded by any trace of the other stages, so far as could be found by thorough search. These beds were, as just mentioned, upon soils of high water-retaining capacity. Furthermore, as brought out by two extreme seasons, in a very dry summer (1897) the uredo stage appeared upon some beds which never showed it before or since, while in a season of excessive rainfall (1898) some of the places most affected with red rust in other years had only the teleutospores late in the season.

These facts were regarded as showing the indirect relation of the rust fungus to water. In the dry seasons and upon the drier soils lack of moisture unquestionably reduced the vitality of the asparagus plants. Consequently, they became more susceptible to disease and suffered in inverse proportion to the amount of soil moisture available. As to the direct relation of the parasite to water, the conclusion must be drawn from the observations of these investigators that the host-plant, depending upon the soil, felt the effects of unusual dryness to a more serious extent than did the parasite, thus turning the balance more strongly in favor of the latter; while, on the other hand, in a wet season or heavy soil the asparagus derived more benefit from such conditions than did the fungus, and thus the activity of the latter was checked. In other words, the fungus appeared to obtain sufficient moisture for its requirements even in the dry season, and received no proportionate invigoration from an excess of moisture in seasons of abundant rainfall. It is also indicated by these observations that the uredo stage is characteristic of conditions favorable to the fungus, while in the unfavorable seasons or localities no develop-

ment of the parasite took place until the plants began their natural loss of vitality at maturity, and under these conditions, when little nourishment was left for an active parasite, only teleutospores appeared.

Another side of the relation of *Puccinia Asparagi* to water was brought out particularly by Sirrine,[2] who, from his observations in New York, was led to conclude that the relation of the rust to atmospheric moisture in the form of dew or fog was the most important factor of this nature in the development of the disease. In the cases described by this writer the progress of the fungus seemed to be accelerated by excessive dew-fall, while with the absence of the latter the rust was less prevalent. In an asparagus bed upon a sloping hillside, for instance, the most rusty portion was at the base, decreasing with the rising grade. It has also been frequently observed that asparagus growing in the shade, as where a tree stands in the midst of a bed, remains free from rust when all about it is dead with the disease. This fact shows certainly that the protection thus afforded prevents infection by the fungus, and can be explained only on the ground of the prevention of dew being deposited. Stone and Smith maintained, however, that under ordinary conditions no such differences existed in their section as were observed by Sirrine, since some of the least rusted beds were in regions most subject to heavy dews, and in the case of asparagus growing on a slope, that at the bottom was likely to be least affected, on account of the usually heavier soil there. They held in regard to the influence of dew that, "when plants are not resistant enough to stand uredospore infection, it is not difficult to understand how this might take place, but the presence of any amount of dew fails to infect some beds in this state;" the beds referred to being those in heavier soil.

In the writer's opinion both of these theories as to soil and atmospheric moisture were correct, but modified by local conditions. In Massachusetts asparagus is grown upon a great variety of soils and showed from the first more decided differences in susceptibility to the rust than in any other section. These conditions were studied with great thoroughness by field observation and mechanical analysis of soils all over the state, and the conclusions arrived at have been

[2] Bulletin 188, N. Y. (Geneva) Exper. Station.

repeatedly verified from year to year. In New York and New Jersey large asparagus districts exist of practically uniform soil and of the nature characterized by the Massachusetts investigators as most favorable to rust. In these districts the disease became exceedingly virulent at first and completely exterminated the original beds, without regard to slight differences in soil or other features which are well marked in the new plantations of the same districts, now that the severity of the attack has somewhat subsided. Since dew is necessary for infection, it is but natural that where other conditions were equal, the progress of the disease should be temporarily marked by varying amounts of atmospheric moisture, but it must be said that throughout the eastern states dew is so generally abundant, even in the driest seasons, that nothing of permanent value can be credited to this relation. That dew is absolutely necessary to the development of the fungus seems proved from the effects of tree shade in asparagus fields, and this is the direct water-relation of this parasite.

Conditions in California with respect to soil and atmospheric moisture are totally different from those of any eastern state. On account of the long, rainless summers, marked differences in the natural conditions of various parts of the state, and the prevalence of irrigation, any question having to do with moisture problems can be followed with a degree of precision quite impossible under the natural conditions of the east. This refers particularly to the degree of dryness obtainable, both of soil and atmosphere, a degree approximated nowhere else in the country save in the adjoining semi-arid states. The principal asparagus-growing section of California has proved to be especially well-adapted to a study such as that herein described, and a description of this portion of the state must be given at this point.

If in the accompanying map (*fig. 3*) a triangle be imagined between the cities of Sacramento, Stockton, and Antioch, it will include, at a safe estimate, 5000 acres of asparagus. This country is at the confluence of the two great rivers of California, the Sacramento and the San Joaquin, together with a smaller stream, the Mokelumne, which enters the angle formed by the other two where they join. These rivers do not run directly into one another, but form, in the triangle just mentioned, a delta, composed of an intricate network of

channels, sloughs, and low islands. By extensive dredging and levee work much of this extremely fertile country has been reclaimed and brought into cultivation. The soil is a mixture of peat and

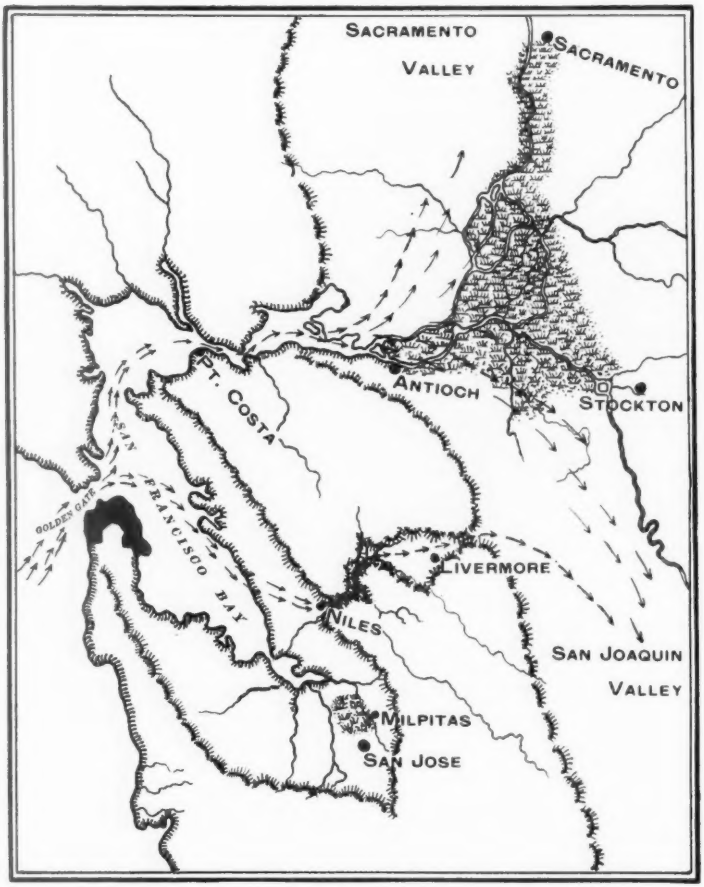

FIG. 3.—Map of central California, showing asparagus districts.

river sediment in various proportions, from almost pure formations of each to an equal mixture of the two. After reclamation and continued cultivation the level of these islands gradually sinks, and they become saucer-shaped, several feet below the river level outside

the levee (*fig. 5*). The soil is naturally full of moisture, but with levees, drainage, and rainless summers it may become extremely dry unless irrigated. Fires frequently occur in the peaty formation and cause serious damage. Irrigation is a simple matter in most cases, requiring only the placing of gates in the levee to admit and shut off the water.

While this country would at first seem to be one of excessive atmospheric moisture, the reverse is true in summer. Much of the reclaimed land becomes extremely dry, but most important is the position of this region directly at the opening of the great interior valley of California into San Francisco Bay and the Pacific Ocean (see *fig. 4*). Through this opening, formed by the Golden Gate at San Francisco and the Carquinez Straits at Port Costa, there blows in summer the strong, steady, so-called trade wind, coming in from the west, passing up through the straits, and then dividing north and south in response to the currents caused by the extreme summer heat of the great interior valley. In this asparagus country there occurs almost every day in summer a strong, dry, west wind which rises early in the morning and quickly dries what little dew may have been formed, except in sheltered spots. This wind, therefore, is an important and perhaps the chief factor in the amount of dew formation. Across the lower left corner of the triangle, where the wind is most constant, there is practically no dew in summer. Approaching the other two angles there is more, though much less than any eastern section.

At various points on the margin of San Francisco Bay are other asparagus districts, most important of which is that near Milpitas, comprising some 600 acres. This is situated, as may be seen, in a sort of pocket at the lower end of the bay, surrounded by high hills on both sides (*fig. 6*). The wind current coming in at the Golden Gate blows across the bay quite constantly and has a tendency to turn south toward Milpitas and the Santa Clara Valley below, but at Niles it is diverted into the interior valley through the Niles Cañon and Livermore Pass, which open through the hills at this point. Without lengthening this already extended description, it need only be said that this produces a condition at Milpitas much similar to that in the East as regards dew. Atmospheric moisture from the

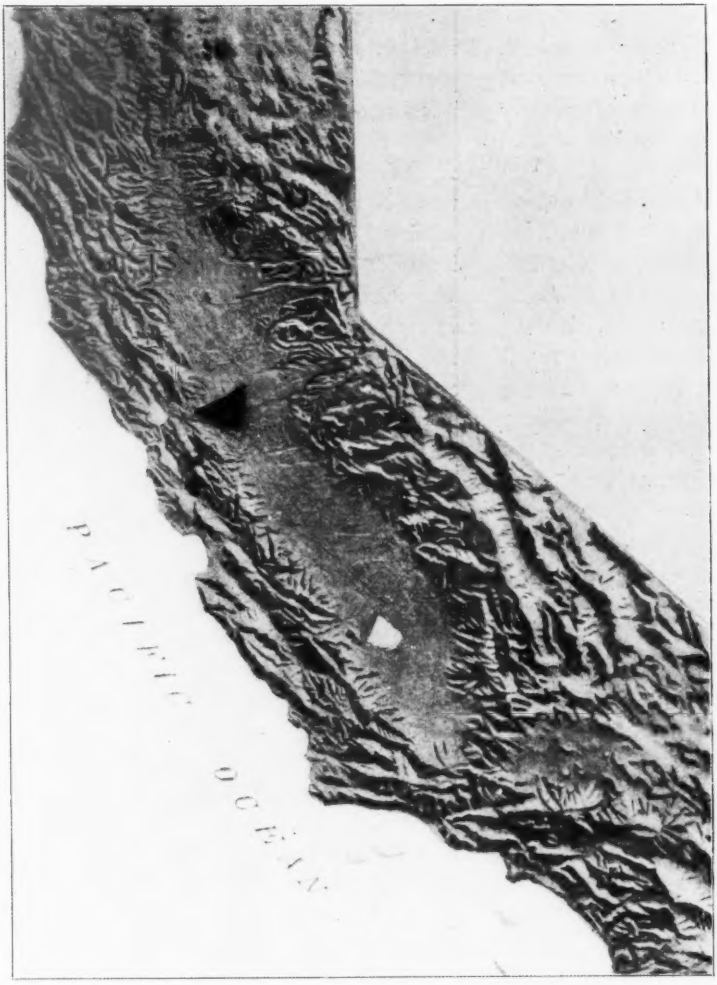

FIG. 4.—Relief map of California, showing the great interior valley and position of asparagus districts; Niles-Livermore Pass also indicated. Adapted from U. S. Department of Agriculture Yearbook, 1902.

FIG. 5.—Typical island country, showing low level ground surrounded by levee.

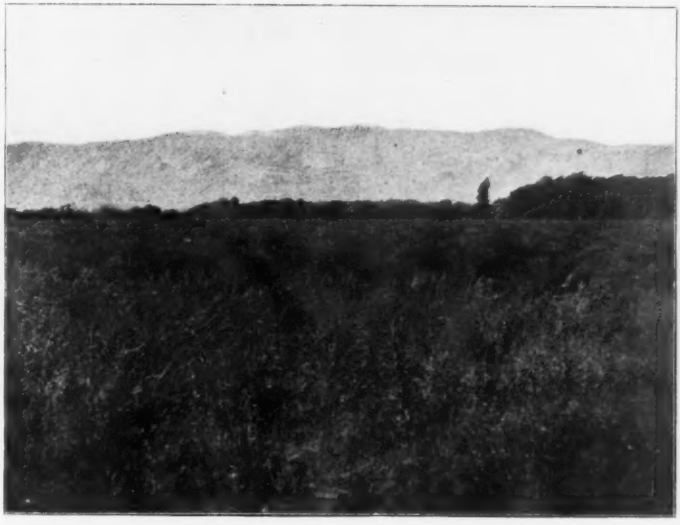

FIG. 6.—Typical asparagus field at Milpitas; high hills in distance.

nearby bay and ocean is abundant; heavy dews are frequent in summer and remain until late in the forenoon. The soil here is also more like the typical eastern asparagus soils, being of a light sandy nature, drying excessively in summer unless irrigated, which can be easily accomplished from artesian wells.

In both these districts the aecidial stage of the asparagus rust is extremely abundant in spring, following the winter rains, the condition shown in *fig. 2* being of ordinary occurrence in large areas. As the season progresses, this is followed at Milpitas with the usual development of the rust about as seen in the east; the aecidia are followed by an epidemic of uredo on the main cutting beds, which kills the tops quite generally and turns finally into black rust as a final stage. In the river country the progress of the disease is not so regular. As the season changes from moist spring to dry summer, the effect shown in *fig. 7* becomes evident. This is an aecidial patch upon a young stalk which started in the usual manner, but as the air became drier and dews less abundant its development was checked. Soil moisture was abundant, but it is seen from this not only that the fungus requires atmospheric moisture for its spore-germination, but that a certain degree is also needed for the development of spores from the aecidial patches. At this stage the mycelium is

FIG. 7.—Aecidial patch checked by lack of atmospheric moisture. Grand Island, Calif., July 13, 1903.

FIG. 8.—Aecidial patches drying out without developing spores; plant green and vigorous. Bouldin Island, July 28, 1903.

vigorous and ready for development, as may be proved by placing such a stalk in a moist chamber, when the "cluster-cups" break out in great luxuriance. This is another direct water-relation of the rust, therefore, being apparently a provision for developing aecidiospores only when conditions are favorable for germination. In the dry, windy districts such aecidial spots remain in this condition far into the

FIG. 9.—Uredo infection on green, vigorous stalks, checked and changed to teleuto by lack of atmospheric moisture. Bouldin Island, July 28, 1903.

summer. Finally, they pass into the state shown in *fig. 8*, the original aecidial areas drying out, leaving a feeble development of mixed uredospores and teleutospores about the edges.

Through the period of midsummer, from June to September, but little trace of rust can be found in most of this country. Careful search, however, reveals here and there on volunteer growth in sheltered nooks the condition shown in *fig. 9*. These are green

vigorous stalks, each with a single infection contracted earlier in the season, which now appears as an almost pure teleutospore formation directly on the green stalks. The value of these spores as reproductive bodies is doubtful, as they will not germinate at any time during the summer. Apparently this is rather the form assumed by the fungus under unfavorable conditions, when infection could not take place, producing only the resting, teleuto stage. If such a stalk be placed in a moist chamber, there immediately breaks out at the outer edge of the infected area a circle of uredosori, with spores capable of immediate germination. The same occurs in nature later in the season as the dew becomes more abundant. Here again is shown the same relation to atmospheric moisture in the case of uredo development, proving that the fungus not only requires moisture for the germination of its spores and for infection, but has the same requirement for the production of spore forms capable of immediate germination. Experiments by the writer show that both the aecidiospores and uredospores of this fungus are comparatively short-lived, but that the teleutospores are capable of lying dormant for long periods and have a strong relation to the effect of frost in their germination. This also shows the teleuto stage as not necessarily a fall rust, but as occurring regularly under other conditions extremely unfavorable to the further development of the fungus.

It is to be understood that these stages described are not individual cases, but the regular development of the asparagus rust in such a district as this. In September moisture becomes a little more abundant, varying locally with the amount of irrigation and other conditions, and now begins the regular uredo epidemic. This starts invariably in the island country in corners and low places sheltered on the west, such as are shown from actual experience in *figs. 10, 11, 12, 13*. These are all of the same nature and represent spots where uredo infection started two or three weeks before the main beds in the open were affected. It is scarcely necessary to say that such places will be avoided by growers in the future.

In the latter part of September the rust gradually works out into the open fields. The trade wind is now subsiding, but blows fitfully for days at a time. The disease still seeks shelter from this drying influence and appears first on the east side of north and south rows,

FIG. 10.—Corner of asparagus field sheltered from wind by willows and levee. Bouldin Island.

FIG. 11.—Bouldin Island schoolhouse, surrounded by asparagus fields and harboring rust on east side.

or in the sheltered places among the thick tops. Here it starts in scattered spots, each very distinct, and if uninterrupted continues spreading until late November, passing into the teleuto stage in the ordinary manner. The feature shown in *figs. 14* and *15* is, however, one of the most remarkable. In this particular instance the rust started in the uredo form in the scattering manner just described. *Fig. 14* is in a mass of tops sheltered by taller growth toward the west,

FIG. 12.—Old slough bed at Sacramento, with asparagus to left; starting point of rust. August 14, 1903.

and *fig. 15* is the east end of an east-and-west row. Just as this was well started (the condition all over the district was mostly the same), the wind revived in a very dry form and blew steadily for a number of days, with quite cold nights. Immediately the uredo rust on the green stalks turned to teleuto, the rust stopped spreading, and the fields looked exactly as though a fire-brand had been thrust into the green tops here and there, producing a black, dead spot in the green, healthy growth. The tops being still growing, new growth came up through, and the fields were spotted with these perfectly black, dead, teleuto-covered patches, surrounded by and in contact with

green healthy growth. *Fig. 16* shows a branch from the edge of the dead spot with pure teleuto development on the green thrifty branches. This condition lasted so long as the wind continued, then gradually reverted to uredo infection, and the tops all became affected. This shows more strikingly than anything else the effect of real atmos-

FIG. 13.—Asparagus at Sacramento, sheltered on west by trees; same effect as in *figs. 11, 12, 13.*

pheric dryness upon *Puccinia Asparagi* at this stage of its development, and the function of the teleuto form.

At Milpitas, where dew was quite abundant, though probably scarcely as much so as in the east, and no summer rains occurred, no such effects could be seen. Early in September everything was badly rusted. Even here, however, one feature in connection with the dew-relation is marked. This is the progress of the rust from top to bottom of the stalks, seen in all cases of the disease in this state. *Fig. 17* shows the condition well along in the season, the

FIG. 14.—Dead, rusty spot in green asparagus tops where fungus was checked by wind and changed to teleuto form. Bouldin Island, October 20, 1903.

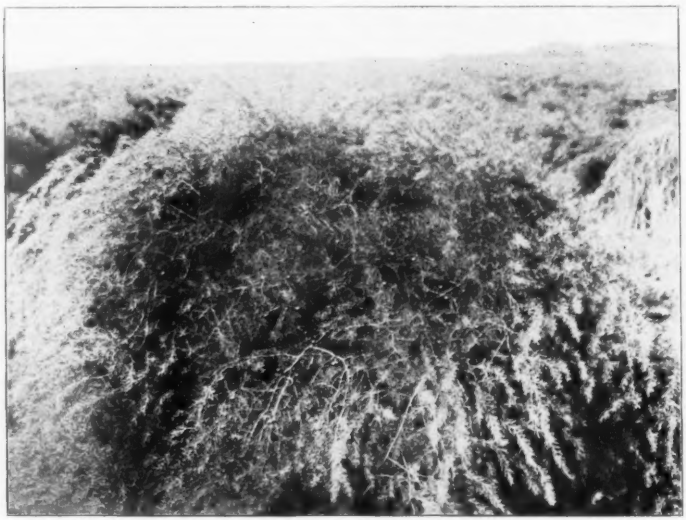

FIG. 15.—Same as *fig. 14*.

top shading and protecting the lower portion. *Fig. 18* shows the bed still later, a condition which in beds well cultivated often lasts until November. The writer has considered that this feature may be due to the absence of rains to drive the spores more rapidly down

FIG. 16.—Teleutosori on green branches at margin of spots as in *figs. 14* and *15*.

through the tops, as he has never observed it in the east. By the means shown in *fig. 19* the rust can be absolutely prevented in California, although in Milpitas the covering must be thicker than on the islands, where one thickness of light cheese-cloth is sufficient.

It may also be said here that from the writer's observations he has concluded that heavy rainfall has little to do in any section of the country with producing infection by the rust, since there is evidence to show that by this means the spores are actually washed from the smooth surface of the plant to a great degree, rather than being afforded opportunity for germination and infection. A copious, misty dew, remaining until late in the forenoon on the thick asparagus

FIG. 17.—Effect of rust at Milpitas, working from above downwards. September 23, 1903.

tops, appears to be the most important factor in producing infection. Experiments with uredospores, placed out of doors on dry glass slides night after night in various situations, support this view, as well as extended field observations. During rain the spores are washed from the slides and carried away. This would not occur so entirely upon the plant, but is true to a very large extent. During nights of very light dew no germination occurred. With slight dew, drying away early in the day, germination started, but the germ-tubes dried up before they would have had time for infection. Most

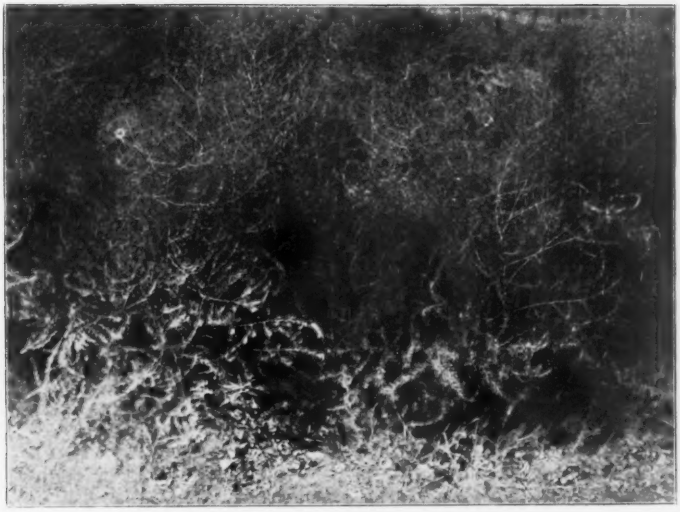

FIG. 18.—Condition late in the season of many California fields; green strip at bottom. November 1, 1903.

FIG. 19.—Tent over asparagus; tops just growing up. Bouldin Island, July 14, 1903.

of these dews seem to form just before sunrise in California, so that they exist only a short time. On misty nights, with heavy dew, a most vigorous germination takes place, easily sufficient to produce infection. It has even seemed to the writer that germination in this way is more vigorous than in drops of distilled or tap water placed on the slide, though no exact comparisons have been made.

Something remains to be said as to the influence of soil moisture upon the rust in California. In the island district the wind effects are so absolute that all other features are of secondary importance. Soil moisture increases the amount of dew, and since almost all this country has abundant natural subirrigation, it is desirable to keep the surface as dry as possible. In the case of one plantation, particularly, situated in the strongest wind belt and where the nights were particularly dry, no rust whatever has developed, though in a center of infection, although the soil became so dry through neglect that cracks opened six inches wide and four feet in depth, and the asparagus roots were almost killed. It should be fully understood, however, that in this case there was absolutely no moisture in the air to germinate spores. A sheet of tissue paper lying on the ground would be as dry and crisp at sunrise as at noon. Such conditions are never approximated in the east.

At Milpitas, with considerable dew on all the beds, differences in soil moisture are more apparent. Some of the beds here are left unirrigated and uncultivated in summer and become extremely dry. In these the rust makes much more rapid headway than in the irrigated beds, and the tops are killed to the ground, while the others still have the green bottom (*figs. 17, 18*) late in the season. It is a general principle, in fact, that in this district, where conditions resemble those of the east, except for the absence of summer rain, the driest beds rust first and most completely, while those kept wet throughout the summer are the latest and least affected. This could not be shown more plainly than by the field in which *fig. 20* was taken. In this case a stream of water was being run past the end of a very dry asparagus field for irrigating lower down. When the whole field back to the right was dead with rust, the end plants in each row, next the water, were green and vigorous, as shown in the illustration. It is difficult to imagine how more absolute proof

could be found than this. *Fig. 21* is along the same line, showing a low corner of a hundred-acre asparagus field, which portion remained green much after the tops in the drier portion of the field were dead. The water from irrigation accumulated here in the rusty season, with the effect described and illustrated.

FIG. 20.—Effect of irrigation in region of dry soil and abundant dew. Near San José, Calif., August 20, 1903.

The water-relation of *Puccinia Asparagi* may be thus summarized:

DIRECT RELATION.

By direct relation is meant the effect of moisture (necessarily atmospheric, except possibly in connection with the germination of the teleutospores, which has not been touched upon) acting directly upon the spores or mycelium of the rust. This relation has proved to be of foremost importance when absolute conditions prevail. It has been attempted to show:

That dew is of absolute necessity in infection by the rust and of more importance than rain.

That without moisture of this sort no infection can take place, regardless of all other conditions.

That the effects of atmospheric dryness are not limited to the spore-germination, but produce the following effects upon spore production in cases of previous infection: Aecidial development is checked, no "cluster cups" appear, and the mycelium remains dormant for some time; if moisture conditions occur, spores are at once

FIG. 21.—Showing same as *fig. 20*. Milpitas, August 20, 1903.

produced, otherwise the mycelium finally dies out. Uredo development is similarly checked and changes to a production of teleutospores in the sori already formed, without regard to season or condition of the host; with moisture uredospore formation begins again at once.

That the teleuto stage is a provision for surviving any condition unfavorable to the fungus, whether of food supply, moisture, temperature, or resistance by the host, without regard to season.

That extremes of atmospheric moisture conditions are insufficient in most sections of the country to bring out or make effective this direct relation.

INDIRECT RELATION.

By this is meant the effect of moisture acting upon the parasite through its effect upon the host, and limited therefore to soil moisture. It has been attempted to show in this respect:

That under any but very unusual conditions of atmospheric moisture the indirect relation is of greatest importance.

That an abundance of soil moisture during the summer has a marked effect in retarding the development of this fungus by giving the host greater vitality and resistance.

That this is shown by the effects of the varying summer rainfall in different seasons, by the differences in the water-retaining capacity of different soils, and by the effects of irrigation.

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DELTA AND DESERT VEGETATION.

DANIEL TREMBLY MACDOUGAL.

(WITH SEVEN FIGURES)

THE systematized discussion of the deserts of North America recently attempted by Mr. Coville and the author[1] made it obvious that the southern extension of the Nevadan-Sonoran desert in Sonora and peninsular California around the head of the Gulf was practically a *terra incognita* to the naturalist.

The waters of the Gulf have been surveyed and the more prominent features of the shore lines traced, but since this work was done thirty years ago, the charts, originally made from data collected by "Commander" George Dewey in 1873–75, are sadly in need of revision, especially in the region contiguous to the mouth of the Rio Colorado. The positions of the prominent hills and mountains visible from the sea have been plotted as range marks for the navigator, but the maps bearing the results are difficult of interpretation by the explorer on land.

A fair share of attention has been paid to the animal life of the river and Gulf, but the extensive areas around the mouth of the river and the head of the Gulf have so far practically escaped investigation. These regions offer difficult problems of transportation and subsistence to the explorer. The southern part of the delta includes vast areas of muddy salt flats cut by a labyrinth of shallow pools and channels, and joining directly the desert slopes and plains of Baja California and Sonora. The water in the lower course of the river is brackish for a distance of 30^{km} from the sea, while other sources of water are uncertain and widely separated, the tropical sun forming an additional factor to test the endurance of the unaccustomed traveler. In running the boundary on the long northwestward slant of the Arizona-Sonoran line after the Gadsden Purchase Treaty, the commission found it necessary to haul water nearly 200^{km} to meet the needs of its camps. The trail which runs near the bound-

[1] COVILLE, F. V. and MACDOUGAL, D. T., The Desert Botanical Laboratory of the Carnegie Institution. November, 1903. Washington, D. C.

ary across a typical portion of the desert mesa was the route followed by Mexican prospectors rushing to the Californian gold fields in 1849, and in the waterless stretch of 150^{km} between Quitovaquito and Tinajas Altas may be counted over four hundred small circles and crosses of loose stones by the side of the trail, grim evidences of failures to negotiate this formidable "Jornada del Muerto."

Attempts to penetrate the desert directly from the coast have met with equally serious difficulties. The shore is fringed with mud flats many kilometers in width, and numerous sand bars bare at low water; the tides rise 4–10^{m} and produce currents that run 4–8^{km} per hour, forming waves or bores that sweep up the river, at times endangering all craft not in protected anchorages. But few sheltered anchorages are to be found in the upper Gulf, and nearly all of these are far from a supply of fresh water. The few expeditions to this region in which attention was paid to the flora are easily recounted.

Colonel Andrew B. Gray traversed the desert from the international boundary to Adair Bay in 1854, discovering the singular parasitic *Ammobroma Sonorae* Torr.,[2] which fastens to the roots of Franseria and Dalea at depths of 60–120^{cm} in the sand, and sends its fleshy stems to the surface, on which the flowers appear to rest.

Dr. E. Palmer traveled southward from Yuma to Lerdo near the head of tidewater in 1889, and collected about two dozen species of plants,[3] but no general account of the expedition is available.

Descriptions of a number of the plants are to be found in the accounts of the boundary survey,[4] in which but little attention, however, appears to have been paid to the flora of the delta.

T. S. Brandegee[5] made a long journey overland, in the same year in which he traversed Baja California, for a distance of several hundred miles northward to San Quintin in about the same latitude as the southernmost point reached by my own expedition. However, he did not reach the country east of the main divide north of San Luis Bay, 300^{km} south of the mouth of the river.

[2] TORREY, J., Ammobroma, a new genus of plants. Ann. Lyc. Nat. Hist. N. Y. **8**: June 1864.

[3] ROSE, J. N., Contrib. U. S. Nat. Herb. **1**:27. 1890.

[4] Report on U. S. and Mex. Boundary Survey, Emory **2**:21. 1859.

[5] BRANDEGEE, T. S., A collection of plants from Baja California, 1889. Proc. Calif. Acad. II. **2**:—. 1889.

Mr. Edmund Heller made some explorations and zoological collections for the Field Columbian Museum, February–December 1902, in which the western slopes of the Santa Catalina, San Pedro Martir, or Calamuie Mountains and of the Hanson Laguna Mountains were traversed. Mr. Heller crossed the main divide in about latitude 31° 30′, south of the main elevation of Calamahuie, to Parral, which lies about 600^{m} above sea level. One degrée to the northward the main range was again crossed at San Matias Pass and his expedition reached the bay of San Felipe. The account of this work contains notes on the occurrence of many important plants, including the giant cactus and the Washington palm.[6]

The author organized an expedition to this region early in the present year, under the joint auspices of the Desert Botanical Laboratory of the Carnegie Institution, and of the New York Botanical Garden. In accordance with plans made a year previously, Mr. G. Sykes, civil engineer, of Flagstaff, Arizona, proceeded to Yuma in November 1903, where the construction of a small sloop, 9^{m} in length with 2.4^{m} beam, was begun and which was brought to completion late in January 1904. This boat was of a flat-bottomed design suitable for floating down the muddy shallows of the river, and was furnished with a centerboard for use in sailing the rougher waters of the Gulf, being rigged with a mainsail and jib.

In addition to the camp equipment, which included means for storing and carrying fresh water, and a special form of portable canteen, provisions, compasses, binoculars, cameras, aneroids, thermometers, hygrometers, and other material to a total weight of about 500^{kg} was taken aboard. The party included Prof. R. H. Forbes, Director of the Agricultural Experiment Stations of Arizona, and an assistant, in addition to Mr. Sykes and the author. A general narrative in which the detailed movements of the expedition are given has already been published[7] and need not receive further attention in this article.

[6] ELLIOT, D. G., A list of mammals collected by Edmund Heller in the San Pedro Martir and Hanson Laguna Mountains and the accompanying coast regions of Lower California. Field Columbian Museum, Publ. 79. Zoological Series **3**: no. 12. 1903.

[7] MACDOUGAL, D. T., Botanical explorations in the southwest. Jour. N. Y. Bot. Garden **5**:89. 1904.

THE DELTA.

The expedition cast loose from the shore at Yuma at noon on January 28, and within a short distance below the sand bluffs on either hand curved away from the stream, and we were fairly in the great delta which extends from this point to the Gulf of California, a distance of about 140^{km}; while the coastal plains on the western side of the Gulf embrace mud flats that constitute an actual extension of the delta 50^{km} further. This delta probably offers more varied and striking features of natural history than any other watercourse in North America. The river which has formed it rises in the perpetual snows of Utah, Wyoming, and Colorado, and runs 2500^{km}, chiefly through arid regions, before it empties into the upper end of the subtropical Gulf, into which it carries sixty million tons of sediment yearly, building up the delta and extending it seaward at a rate visible to common observation within a single lifetime.[8] Numerous witnesses among the Cocopa Indians, Mexicans, and river men are agreed that the various distinct associations of plants characterized by salt grass, willow, and poplar, have advanced about 12–14^{km} to the southward during the last fifty years.

The portion of the delta near the present course of the river consists of an alluvial plain, not more than 4^{m} above the low-water mark, subject to constant bank erosion, shifting, and remaking of the soil, cut in all directions by old channels existing as bayous and sloughs, and flooded at high water in May, June, and July. Almost pure formations of willow and poplar (*Populus mexicana*) cover many square kilometers and furnish food for thousands of beavers that burrow in the banks. The poplar is thickly infested with a mistletoe (Phoradendron), and fungal parasites are abundant. Large areas are occupied by the arrow-weed (*Pluchea sericea*), and mesquite (*Prosopis velutinea*), and the screw-bean or "tornilla" (*P. pubescens*). Two or three species of Atriplex are also to be found in sections in which the action of the water prevents the establishment of the woody perennials of greater size. In the upper part of the delta a cane (Phragmites) fringes the channel, and its closely interwoven roots act materially in preventing erosion of the banks.

[8] FORBES, R. H., The Colorado river of the west. Univ. of Ariz. Monthly **6**: 112. 1904.

In the lower part of the delta, where the river is affected by the spring tides, the cane is partly replaced by a cat-tail "tule" (*Typha angustifolia*), which not only lines the shores for many miles, but extends back some distance on areas free from trees, forming dense masses

FIG. 1.—Scene on right bank of Rio Colorado, Baja California, a few meters from the margin of the stream, 10$^{km.}$ below Yuma; the conchoidal fractures of the clayey mud are 30–35^{cm} in depth; Salix and Populus in background; Station 1 of hygrometric observations.

that afford shelter for a number of animals, including a peculiar subspecies of a small mountain lion.

Large areas throughout the delta which were not covered by trees bore wild hemp (Cassia?) in great abundance. The slender stems reach a height of 3–4^{m}, branch profusely above, and bear numerous pods. At the time of our visit, the plants which were annuals were

dead and dry, still retaining the seed pods, and progress through one of these plantations was accompanied by a shower of seeds which results from any disturbance of the plant. The clearings also furnished suitable conditions for a plant with a deeply buried bulb, probably a Calochortus, which is eaten by the Cocopa Indians under the name of "chech," and also forms an important article of food of the sand-hill crane, and of the wild hogs that infest the tules.

The forests of willow and poplar begin to lose density at a distance of 50–60^{km} from the Gulf, the willows extending farthest toward salt water, a few being seen near the mouth of the Hardy branch of the Colorado. Beyond these are the mud plains, the portions not actually subject to erosion being thickly covered with salt grass (*Distichlis spicata*) and *Cressa truxillensis*, and bearing small clumps and isolated specimens of salt bush (Atriplex), mesquite, and screw bean. Such areas are inundated at the highest tides; consequently the soil solutions are heavily charged with salts, and whitish alkaline crusts appear during the winter dry season.

The floods of spring and early summer from the rains and melting snows of the headwaters region of the river raise the level of the water until it flushes the innumerable old channels and covers the greater part of the delta. Most of the herbaceous species make their annual growth after the waters have subsided in July. Other species, which are less affected by the lower temperatures and low relative humidity of the winter season, are set in action by the favorable conditions of March and April, and come into bloom at this time, thus making two distinct seasonal groups of annuals.

The main stream of the river cuts directly into the gravel plain or mesa of Sonora at four points on the eastern margin of the delta, and here are to be seen the striking contrasts of the isolated xerophilous plants of the dry gravelly soil of the desert within a few meters of the pure dense formations of the muddy soil of the alluvial plain of the delta (*fig. 2*). In places the creosote bush (Covillea) descends the gentler slopes to the margin of the moister soil near the margin of the channel, accomplishing a growth which carries it to a height of over 7^{m}, the maximum size for the species.

The above description applies most directly to the eastern and southern portions of the delta, which may be observed in the descent

of the river, but it by no means exhausts the interesting features of the region. If the low-lying contiguous areas to the westward capable of being flooded are included, the delta may be said to have an area approximately equal to the state of Connecticut. One arm extends over 200^{km} to the northwestward and includes the Salton Basin, with its exposed bottom more than 130^{m} below the level of the sea. Although the summer floods of extreme height find their

FIG. 2.—View of Rio Colorado at a point where it cuts into the desert mesa of Sonora a few kilometers south of international boundary; looking downstream; Populus and Salix on right bank; dense forest of Populus in background on left bank; portion of mesa in foreground on left bank with Covillea, Stillingia, and Ephedra; Station 3.

way by old channels into this basin, creating a temporary lake of great extent, yet the district affected must be classed as desert, since the highly saline character of the soil and prevailing low humidity and precipitation support representative types of vegetation (*fig. 4*).[9] Other basins ordinarily dry, with saline deposits, are to be found in various parts of the depressed area, which has the characteristics of a sea-floor of comparatively recent date.

[9] See also COVILLE and MACDOUGAL, The Desert Botanical Laboratory of the Carnegie Institution (November 1903), pp. 21–22. *pls. 23–26.*

Many parts of the delta and of the adjoining districts in the deserts of Sonora and Baja California show traces of recent earthquakes and of volcanic action, a tract 2 by 10^{km} being now occupied by a number of active mud volcanoes.

FIG. 3.—View to southward on floodplain of Rio Colorado below mouth of Hardy's branch; Range Hill in distance; carpet of *Cressa truxillensis* and *Distichlis spicata;* Prosopis scattered over plain, which also shows great quantities of driftwood.

The Cocopa Mountains rise directly from the delta to a height of over 1300^{m}, and their granite slopes support an island of desert vegetation of the types induced by low humidity and precipitation.

DESERTS.

The arid region east of the delta, extending southward from the Gila River, consists principally of long gentle slopes or sandy gravelly plains rising gradually toward the interior, and broken here and there

by a succession of low mountain ranges, such as the Agua Dulce, Pinacate, and Santa Clara Mountains. The soil is particularly subject to the action of the wind, but the irregular consistency of the sand allows the formation of moving dunes or "sables" in a few localities only near the delta. Mounds of a few meters in height, held together by the roots of Ephedra, Covillea, and other shrubs, are numerous, however, such mounds being due either to the erosion of the soil around them, or to its accumulation and retention by the

FIG. 4.—View in Salton Basin, California; the surface of the soil is thickly incrusted with saline matter in the open spaces; the vegetation consists chiefly of Spirostachys and Atriplex.

clumps of plants. In addition to the few herbaceous annuals which arise during the season favorable for growth, the principal types are perennials with spinose branches and reduced deciduous leaves, although a few species with hardy leaves are included. *Ephedra*, *Gaertneria albicaulis*, *Oenothera clavijormis*, *Lupinus mexicana*, *Abronia villosa*, *Astragalus Vaseyi*, *Plantago scariosa*, *Langloisia Schottii*, *Stillingia annua*, *Asclepias subulata*, and *Fouquieria splendens* are typical examples; while a few forms with deeply lying bulbs are also found here, including *Hesperocallis montana* (*fig. 5*).

The character of the portion of the Colorado desert lying within the state of California is the subject of a recent paper by S. B. Parish,[10] and need not be discussed further here. He says, concerning the delta: "the region bordering the Colorado River is too little known to permit exact statements regarding it."

The arid region of Baja California to the eastward of the main divide covers an area of much greater topographical diversity, but

FIG. 5.—View to southeastward from Lerdo, Sonora; the gravel mesa bears scattering bushes of Covillea and Ephedra.

with less rainfall probably than the Sonoran slopes across the Gulf, from which its flora is widely different in general composition. My examination of this part of the country was made from San Felipe Bay, which lies about 60^{km} south of the mouth of the Rio Colorado in latitude 31° N. The western shore of the Gulf between this point and the river is made up of a continuation of the mud-flats of the delta, and has great expanses covered with Cressa and salt grass.

[10] PARISH, S. B., A sketch of the flora of Southern California. BOT. GAZ. **36**: 203–222, 259–279. 1903.

The central elevation consists of the mountain ridge which culminates in the peak of Calamahuie at an elevation estimated at about 3300^{m}. To the eastward it breaks into lofty precipices and steep slopes which have not been surmounted between 30° 30′ and 32° 30′ N., no passes having been found in this wild stretch of 100^{km}. Between the main range and the coast lie numerous minor ranges disposed in labyrinthine complexity, which also have not been explored. So far as available information may be relied upon, no botanist had previously visited this region, and some care was taken to secure living and preserved specimens of the native plants whenever at all possible.

The lower coastal slopes were found to be sandy and gravelly, the depressions and near the shore furnishing suitable conditions for *Lycium Torreyi* and *Parosela spinosa*, which latter becomes a tree 7^{m} in height. *Asclepias subulata* was abundant in clumps, and *Ditaxis serrata* grew on level areas. Other species, characteristic of the lower levels, were *Ibervillea tonella*, *Croton californicum*, *Lupinus mexicanus*, and the curious *Frankenia Palmeri*. The low alkaline pockets reached by the spring tides furnished conditions suitable for *Spirostachys occidentalis*. Covillea, with its enormous capacity of adjustment, extended from near the shore across the entire slope and up the granite mountains through a range of over 600^{m} in elevation. The various portions of the slope between the sea and the first range of mountains supported ocotillo (*Fouquieria splendens*), which attained its maximum height of 10^{m}, palo verde (*Parkinsonia microphylla*), palo fierro (*Olneya tesota*), Bursera, and *Gaertneria ilicifolia*. The streamways leading down from the mountains were inhabited by a number of Eriogonums and euphorbiaceous herbs. A few Opuntias of the cylindrical arboreous type, an Echinocactus, a Mammillaria, and a small Cereus were also seen. *Pilocereus Schottii*, which is found on the mainland far southward, here reaches the greatest density yet observed, forming dense forests, acres in extent. Perhaps the most notable feature from a geographical point of view was shown by the presence of a great tree cactus, having the appearance of *Cereus pecten-aboriginis*. *Cereus Pringlei* is known to be abundant under the common name of "cardon" farther south, but this plant appears to agree with the former, and makes a splendid picture in the arid landscape, finding here its extreme northern limit of known occurrence.

The large number of species with laticiferous juices was especially noticeable, but with the exception of the dozen Cacti no plants with organs for the storage of water were seen, a fact possibly connected with the extremely low precipitation and low water content of the soil at all times. Seeds of a Cenchrus were very abundant and were

FIG. 6.—Desert of Baja California, looking westward from beach north of San Felipe Bay; Opuntia, Covillea, and Fouquiera.

used by burrowing rodents as a means of fortification of the entrances to their burrows, in the same manner that the joints of the "cholla" are employed elsewhere.

A mountain to the southwestward of San Felipe Bay was climbed and a summit reached at an elevation of over 1000^{m}. The granite slopes supported a sparse vegetation of such types as Mammillaria, Ephedra, *Bursera microphylla*, *Asclepias albicans*, *Eriogonum infla-*

tum, Yucca, Agave, and Opuntia. So far as might be estimated by the instruments at hand, the mountain is probably the one on the hydrographic map of 1873–75 designated as a "sharp white peak 4288^{ft}," which had not previously been ascended, and still bears no name.

METEOROLOGICAL FEATURES.

Data bearing on the climatic conditions in the delta and of the contiguous deserts are very meager. Records have been kept at Yuma for a long term of years, and some data obtained at Torres, Sonora, quoted in the recent contribution by Mr. Coville and the author,[11] constitute the only information available. The following table taken from the records of the U. S. Weather Bureau[12] gives the conditions at the head of the delta.

The transcript of the record was furnished by Hon. Willis L. Moore Chief U. S. Weather Bureau.

1903	Jan.	Feb.	March	April	May	June	July	August	Sept.	Oct.	Nov.	Dec.	Total	Normal
Maximum temperature	76	82	90	97	106	112	111	113	112	96	87	80	..	..
Minimum temperature	33	29	38	47	50	60	69	72	59	51	42	34	..	..
Precipitation	..	.23	..	..	..	..	.04	..	.67	.04	..	..	.98	2.98
Average precipitation (1876–90)	.39	.45	.18	.12	.06	..	.13	.40	.13	.21	.35	.64	3.06	..

MEAN RELATIVE HUMIDITY.

8 A. M.

Year	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1903	53.5	62.9	53.3	52.0	61.3	59.9	61.1	68.3	67.4	54.3	46.7	39.5
1904	43.0	45.7	....	....	....	....	....	....	....	....	....	....

8 P. M.

1903	28.0	44.8	23.0	17.0	17.9	17.8	21.7	2.82	30.9	23.7	28.4	24.2
1904	20.7	21.7	....	....	....	....	....	....	....	....	....	....

It is to be seen that the delta and the contiguous districts have an annual precipitation of less than 7^{cm}, and that less than 2^{cm} was

[11] Desert Botanical Laboratory of the Carnegie Institution, p. 23. November 1903.

[12] GREELY and GLASFORD, Report on the climate of Arizona. Ex. Doc. No. 287. Washington. 1891. Climate and Crop service, U. S. Weather Bureau. Report for Arizona Section for 1903.

received during the year 1903, the relative humidity at all times being very low also. The rainfall is distributed throughout the year, so that only a small proportion of the total is received within any month; furthermore, this distribution is irregular in any series of seasons, so that the native plants have but little opportunity of acquiring a

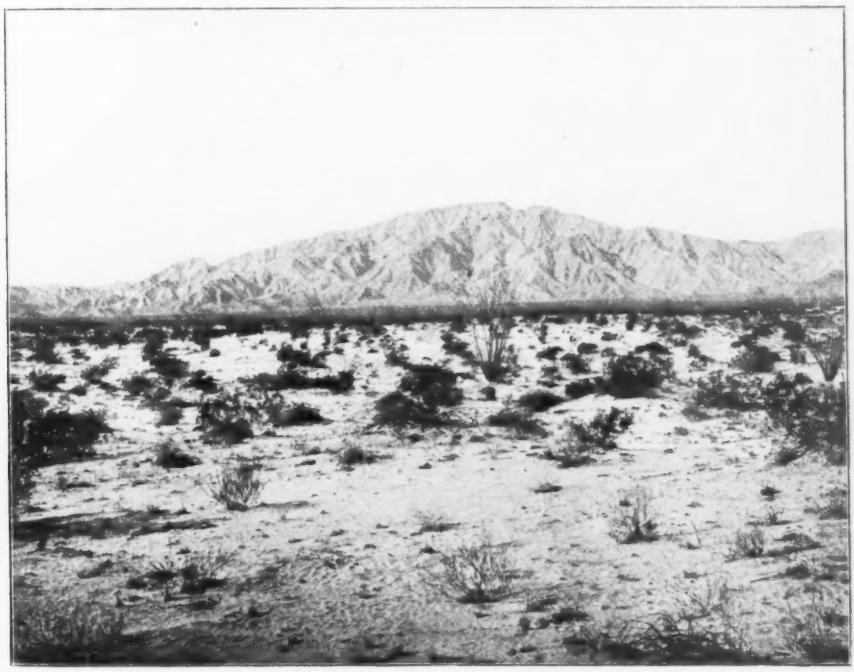

FIG. 7.—Desert of Baja California; view from San Felipe Bay; peak over 1000m high, ascended February 14, 1904, in distance; the sloping plain which rises gradually to the foot of the mountain bears Fouquieria, Ephedra, Covillea, Bursera, Parosela, Parkinsonia, and Cereus.

rhythm of activity in response to the annual supply of moisture, a fact not without its influence on the general anatomical character of the plants, as will be pointed out below. In no part of the country to the southward of Yuma did we find any evidences of a greater rainfall than that given above, upon noting the surface of the soil

and the state of resting vegetation, and no precipitation occurred during the month the expedition was actually in field. Attention is to be called to the table of relative humidity, in which it is to be seen that the minima are very low, yielding averages from 17 to 30 per cent. So far as a general inspection could be relied upon, it did not appear that precipitation had occurred at San Felipe Bay within three months, and it might well have been three times that period since any had been received.

Dr. Edward Palmer visited the Raza Islands in the lower part of the Gulf, 225^{km} northwest from Guaymas, in February 1890, and notes that no rainfall had been received there for more than a year.[13] Nothing can be hazarded as to the extent of the region with this extreme limit of aridity on the Sonoran side of the Gulf, except that it does not include the mesa at an elevation of 300^{m} at Torres, and it does not appear to include the western slope of the central range in Baja California, although no definite information is available. So far as known at the present time, therefore, this region of extreme and constant drought, constituting the most pronounced type of desert in North America, lies on the eastward or lee side of the San Pedro Martir range of Baja California, and includes areas on the Sonoran mainland, the whole being a southern extension of the Colorado desert. It is evident, however, that a further investigation of the region is necessary to determine the exact meteorological status of this area, as well as the general character, derivation and relationships of its flora. The extreme type of strict desert offered by the area in question points to the possibility of finding here the readiest solution of some of the more important problems presented by desert vegetation.

RELATIVE HUMIDITY IN DELTA AND DESERT.

The relatively brief time during which the expedition was in the field made it impossible to secure records of value as to precipitation, although it has been noted above that no rainfall occurred, except perhaps on the higher peaks of the Cocopa Mountains and of the main range in Baja California. A Lamprecht's hair hygrometer was carried, however, and observations were taken daily, the instru-

[13] Contrib. U. S. Nat. Herb. 1:79. 1890.

ment being compared before being taken into the field and after its return with other instruments for standardization. The data given below are corrected results, not direct transcripts from the notebook.

Station 1.

Camp on dried mud flats on shore of Rio Colorado a kilometer below international boundary in Baja California; observations taken twenty feet from margin of bank amid willows and poplars; wind blowing offshore; see *fig. 1*.

Jan. 28	4:30 P. M.	60° F.	17% rel. hum.
" 28	6:30 "	55 "	15 "
" 28	8:00 "	51 "	18 "
" 29	12:45 A. M.	32 "	41 "
" 29	1:20 "	30 "	50 "
" 29	6:00 "	29 "	66 "
" 29	6:25 "	27 "	70 "
" 29	7:00 "	38 "	60 "
" 29	7:40	Sun on instrument	36 "

Station 2.

Camp on small island in great bend 33[km] downstream from Yuma, covered with a dense grove of Salix except at one end.

Jan. 29	4:50 P.M.	61° F.	21% rel. hum.
" 29	7:10 "	37 "	75 "
" 29	8:45 "	32 "	57 "
" 30	2:45 A. M.	30 "	84 "
" 30	5:45 "	26 "	58 "
" 30	7:50	Sun on instrument	35 "

Station 3.

Camp at lower end of high mesa bank below La Grulla, Sonora; observations taken at a point 60[m] from margin of bank 13[m] in height, constituting bank of river, among bushes of Covillea, Ephedra, etc. (*fig. 2*).

Jan. 30	4:40 P. M.	70° F.	19% rel hum.
" 30	4:50 "	68 "	16 "
" 30	7:00 "	54 "	15 "
" 30	8:30 "	48 "	27 "
" 31	6:30 A. M.	44 "	30 "
" 31	7:30 "	45 "	29 "

Station 4.

Noon stop made at point where the river cuts into the Sonora mesa above "Noche Buena" cut-off; observations made at a point corresponding to Station 3, with similar vegetation.

Jan. 31	1:45 P. M.	72° F.	15% rel. hum.

Station 5.

Camp on dry shore in Baja California among willows, poplar, and saltbush, with numerous beaver slides along bank.

Feb. 1	7:00 P. M.	50° F.	30% rel hum.
" 1	8:30 "	44 "	66 "
" 2	6:30 A. M.	41 "	59 "

Station 6.

Group of adobe buildings at Colonia Lerdo, on margin of gravel mesa sloping gradually to the delta, 2^{km} from stream, among mesquite, saltbush, and arrow-weed.

Feb. 3	11:40 A. M.	78° F.	16% rel hum.
" 3	1:30 P. M.	81 "	11 "
" 3	4:15 "	79 "	10.5 "

Station 7.

Camp on eastern shore of river at Colonia Lerdo, among poplar, willow, cane, and tule, 25^{m} from margin of water and 2^{m} above surface.

Feb. 5	7:25 P. M.	64° F.	38% rel. hum.
" 5	7:45 "	64 "	40 "
" 5	2:10 "	67 "	37 "

Station 8.

The data given below were obtained at a number of points on the plain and mountains, near camp on San Felipe Bay, Baja California.

Tent on beach.

Feb. 11	6:20 P. M.	52° F.	42% rel. hum.
" 11	8:20 "	49 "	39 "
" 12	5:50 A. M.	37 "	44 "
" 12	8:00 "	56 "	27 "
" 12	8:35 "	63 "	24 "

In shade of Bursera.

At 76[m] level, 13[km] from shore.

Feb. 13	1:00 P. M.	71° F.	40% rel. hum.
" 13	6:15 "	57 "	41 "
" 14	6:00 A. M.	60 "	33 "

800[m] on mountain.

Feb. 14	8:45 A. M.	69° F.	32% rel. hum.

1200[m] on mountain (*fig.* 7).

Feb. 14	11:00 A. M.	72° F.	32% rel. hum.

Small mountain 100[m] high, 20[km] north.

San Felipe, 8[km] from coast.

Feb. 19	9:45 A. M.	72° F.	18% rel. hum.

RÉSUMÉ.

It is to be seen that the region discussed in the foregoing paper includes a subtropical delta of irregular outline and long extensions, which includes within its outermost boundaries a great alluvial plain subject to floods, bank erosion, and shifting of the soil, and also to the action of salt tidal waters; a mountain range of granite and volcanic rocks over 1000[m] in height; a small area of active mud volcanoes; a depressed region, presumably an old sea-floor, the bottom of which is more than 100[m] below the level of the sea; and the mud flats near the actual mouth of the river. This delta is directly in contact with the gravel and sand desert mesas of Sonora and Baja California.

The portion of the delta subject to the direct action of the floods and tides is everywhere slightly alkaline and varies but little in the general constituency of the soil, supporting a luxuriant growth of vegetation, the more important elements of which grow in pure formations of the greatest possible density. The larger woody plants of this region have their bases submerged in water at a low temperature during the summer season, during which time the crowns are exposed to low relative humidity at temperatures that may be as much as 70° F. higher than the roots. In consequence of this condition many species in the low lands have xerophilous foliage. In addition, a comparatively high concentration of soil salts must be endured during the stages of low water.

An analysis of the flora of the region shows that many of the species of the delta extend down along the coast especially in the

regions with fringing mud banks derived from the river deposits. The greater part of the vegetation of the coastal slopes and plains, however, is made up of species which also extend southward along the shores of the Gulf, and are found but sparingly to the northward.

The vegetation of the Salton basin is subjected to the action of extreme aridity and also of a high concentration of soil salts, comprising types of the most pronounced character, both of halophytes and xerophytes. The elevations included in the delta are dry mountain slopes and support a desert vegetation.

The mesas adjoining the northern part of the Gulf of California appear to offer the most extreme desert conditions in North America. The rainfall at Yuma at the northern extremity of the delta was less than 25^{mm} during 1903, and years have been noted at points farther south in which no precipitation occurred. The entire normal precipitation in the desert in Baja California is probably no greater than the amount of water condensed as dew in eastern United States. The desert apparently extends to the slopes of the central elevation of the peninsula to the westward, which reaches an elevation of over 3000^{m}. This mountain wall probably acts as a barrier which shuts off moisture-laden winds from the Pacific and causes the aridity of the region. The southern and eastern limits of the extreme desert cannot be defined with the information now at hand.

The vegetation of the desert areas in the regions of greatest aridity consists chiefly of types devoid of massive storage organs, and of perennials with laticiferous sap, while a large number of forms secrete volatile oils or exude resinous gums. The determination of the causal relations of these adaptations cannot be made safely by a general interpretation of the aspects of vegetation, but it is to be seen that in a region in which surplus rainfall or ground water never occurs, storage organs would be manifestly useless, and indeed their formation impossible. Species with spinose branches and minute leaves which are quickly discarded during unfavorable periods are abundant. Several species of Ephedra with functionally useless leaves and chlorophyllose stems are included, while Lycium and Frankenia with small succulent easily detachable leaves are highly characteristic of some localities; the last-named species are about

the only species offering anything of the nature of water-storage organs outside of the Cacti.[14]

The region under discussion offers matchless opportunities for comparison of the most highly developed xerophytic types of the desert with the broad-leaved forms of the delta which root in the mud. Midway between the two are the species which stand in the moist soil of the delta, and have foliage suitable to endure the extreme aridity of the air, which constantly blows from the desert over the entire delta.

New York Botanical Garden.

[14] MacDougal, D. T., Some aspects of desert vegetation. Plant World **6**: 249–257. 1903.

BRIEFER ARTICLES.

THE AECIDIUM OF MAIZE RUST.

THE great economic importance of the corn (maize) crop lends special interest to any discovery relating to the habits and development of corn parasites. It is partly for this reason, and partly because it illustrates a method of observation not yet commonly understood, that the following narrative of the discovery of the aecidium of *Puccinia Sorghi* Schw., the common rust of corn, is given here in advance of the season's culture work, of which it forms a part, and which has been undertaken in cooperation with the Bureau of Plant Industry of the U. S. Department of Agriculture.

As corn rust is practically coextensive in geographical distribution with the cultivation of its host, although rarely so abundant and destructive as to attract the attention of the cultivator, and as no aecidium has seemed even in the remotest way to have connection with it, the view has gained ground that either an aecidium is no longer produced in its life-cycle, or that it occurs only in regions where corn was originally wild. In the latter case the aecidium might inhabit some host of restricted range, for all glumaceous rusts with one exception are heteroecious, and the chances, therefore, to detect and prove the genetic connection would be few. I have found that corn rust continues to produce uredospores until very late in the fall, in fact often as long as the corn plants are alive. On October 9, 1901, I tested uredospores taken from plants in the field partly killed by frost, and found that they germinated well in drop cultures. It would seem possible for the rust in northern regions to be wholly distributed by uredospores, beginning in spring from a locality sufficiently far southward to permit the corn plant to survive the winter. However, all these ruminations have taken on a different aspect by the discovery of the aecidium.

The preliminary observations, which provided the necessary inference on which successful cultures were founded, were essentially of the same character as those connected with three-fourths of the discoveries in heteroecism which I have so far made, and are therefore given in some detail as a typical and suggestive example of the method employed in my work.

On June second of the present year, while walking through a thick growth of weeds bordering a cultivated field, I came upon some plants of *Oxalis cymosa* Small, the common form of yellow wood-sorrel in this region, bear-

ing aecidia. The weeds were over two feet high, mostly *Ambrosia trifida*, with many small plants of other species beneath, the Oxalis being abundant. As this aecidium is rarely collected, I began to gather herbarium specimens, and observed that while nearly every leaf on the lower half of the Oxalis stems was infected with the rust over an area of about three feet in diameter, beyond that area it grew less frequent, and was quite absent in four or five feet from the center of the infected area, although the Oxalis plants were equally abundant everywhere in the vicinity. It seemed to me this gave evidence that the teleutosporic source of infection was within the narrow limits of the rusted area. I reasoned that if the sporidia had been blown from a distance, the infection would have been more evenly distributed, and over a larger area. I observed that the lowest leaves on the plants were most thickly dotted with aecidia, and especially those caught beneath the tangle of dead stems from last year's growth. This indicated that the germinating teleutospores must have lain close to or upon the ground, and that the protecting weeds and shrubs had prevented currents of air from materially distributing the sporidia.

I now instituted a search for remains of sedge or grass which might happily show a few teleutosporic sori. Usually one is embarrassed by finding portions of many species, often unidentifiable, but in this case I could find no clumps or stalks of sedge or grass within the infected area, apparently none having grown the previous season, doubtless prevented by the dense thicket of tall weeds, or else they had wholly disintegrated. There was, however, quite a mass of débris deposited by the spring overflow of the near-by river, made up largely of broken cornstalks, but so covered with silt that it was impossible to tell if they had borne rust or not. The cornstalks did not occur beyond the affected area, and so were seized upon as a possible, although very dubious, clue.

The task of testing this inference was neither difficult nor protracted, a piece of good fortune but rarely encountered. Rusted leaves of the Oxalis were taken to the laboratory, about two miles distant, their long petioles placed in a vial of water, and adjusted over a potted plant of corn (*Zea Mays* L.), the whole being covered with a bell jar. On the third day the bell jar was removed.

On the fifth day the corn leaves appeared paler where the spores had presumably fallen; on the seventh day watery pimples began to show; and on the eighth day a few uredosori had opened. In a day or two more hundreds of characteristic sori were displaying a wealth of fuscous spores; and nearly the whole green area of the leaf blades, upon both sides, was so thoroughly rusted as to threaten the life of the tissues.

This prompt and very abundant appearance of the uredo could be interpreted only as the result of the aecidial infection, for corn rust had not yet appeared out of doors, and even if it had, such an unusual attack following closely within the time limit of incubation would be highly improbable. It may therefore be considered proved that the aecidium of *Puccinia Sorghi* Schw. occurs upon Oxalis, and a verification with teleutosporic material can be confidently undertaken in due time.

There are but seven or eight records in literature of the collection of aecidia on Oxalis, and there is little doubt, if any, that in every case the aecidium belonged to *Puccinia Sorghi*. They are as follows:

1876. Collected on *Oxalis Bowiei* Lindl. near Somerset East, Cape Colony, South Africa, by P. MacOwan, and issued in Thuemen's *Mycotheca universalis*, no. 1226. It was given the name of *Aecidium Oxalidis* by Thuemen and described as a new species in Flora **63**:425. 1876. I have seen several specimens from this collection, and can detect no morphological difference between the African fungus and the one from which I raised uredospores. The probability of its being the same species is somewhat increased by the fact that *Puccinia Sorghi* Schw. on cultivated corn was also found near Somerset East by the same collector (Flora **63**:569. 1876) in the preceding autumn.

1877. Collected on *Oxalis violacea* L. at Ames, Iowa, by the writer (Bull. Iowa Agric. College —:167. Nov. 1884). Only a few affected leaves were found.

1887. Collected on *Oxalis stricta* L. at Manhattan, Kan., by W. A. Kellerman (Eliss & Everhart's North Amer. Fungi, no. 2210) and M. A. Carleton (Bartholomew's Kansas Uredineae in Trans. Kans. Acad. Sci. **16**:190). These citations probably represent only one collection. The specimen in N. A. F. agrees with the Indiana collection, except that the host is a different though closely related species.

1889. Collected on *Oxalis violacea* L. at Lincoln, Neb., by H. J. Webber (Bull. Neb. Agric. Exper. Sta. no. 11:333, and Rep. Neb. Bd. Agric. **1889**:211), who speaks of it as rare; and also on the same host at Weeping Water, Neb., about 50 km from Lincoln, by T. A. Williams (Rep. Neb., Bd. Agric. *l. c.*), who reports it as common. I have not seen these collections.

1893. Collected on *Oxalis corniculata* L. at Bozen in the Austrian Tyrol, by J. Peyritsch. This was published by Dr. P. Magnus in the Innsbruck Naturw.-Med. Verein reports for 1894, and described as a new species with the name *Aecidium Peyritschianum*. I have not seen a specimen from this collection, or the published article, but I do not doubt that

the name is a synonym of *Aecidium Oxalidis* Thuem., judging from the brief description in Saccardo's Syll. **11**:215, and from the fact that corn is grown in the region where the fungus was found.

1893. Collected on *Oxalis stricta* L. at Lincoln, Neb., by the Botanical Seminar (Bot. Survey Neb. **3**:10). I have not seen the collection.

1894, 1899. The herbarium of the writer also contains a collection made by Mr. T. A. Williams on July 13, 1894, at Brookings, S. D., and one by Mr. E. Bartholomew on June 5, 1899, in Rooks county, Kan., both on *Oxalis stricta* L., of which there is no published record.

Summing up the evidence, the writer believes that all the above collections can be placed with much confidence under *Puccinia Sorghi* Schw., as representing the aecidial stage of the fungus. It would be interesting to discuss the change in views which this discovery of the aecidium must produce regarding the propagation and dissemination of corn rust, but that can better be left for another occasion.—J. C. ARTHUR, *Purdue University, Lafayette, Ind.*

AN EXPERIMENT ON THE RELATION OF SOIL PHYSICS TO PLANT GROWTH.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LX.

(WITH THREE FIGURES)

IN studies of the relation of soils to vegetational distribution in Michigan,[1] one of the authors found reason to believe that the nature of the vegetation covering any upland area of that region has been determined by the amount of water present in the surface layers of the soil. Furthermore, it was pointed out that, with the exception of swamp margins, the amount of water thus present is dependent upon the physical nature of the soil, especially upon its water-retaining or capillary power, which, in turn, is largely dependent upon the size of the soil particles. The physics of this proposition, together with the literature thereon, is discussed in a paper about to appear in the Annual Report of the Michigan Board of Geological Survey for 1903. It will be necessary to state here only the general fact that the smaller the particles of a soil, the greater will be its water retaining power, and the larger the particles, the smaller this property. Also, the greater the retaining power, the greater will be the power to lift water from a lower level. Thus, clay soils have a great power of

[1] LIVINGSTON, B. E., The distribution of the plant societies of Kent county, Michigan. Ann. Report Michigan Board of Geol. Survey, 1901.

The distribution of the upland plant societies of Kent county, Michigan. BOT. GAZ. **35**:36–55. 1903.

retaining and lifting water, while sandy soils possess this property to a much less degree.

Since the natural soils dealt with in the paper cited differ chemically as well as physically, clay being largely composed of alumina and sand of silica, it seemed wise actually to test by field cultures the hypothesis above referred to. It was desirable that in these cultures the several soils should at the start be chemically the same, while their physical properties alone

FIG. 1.

should differ. To this end crushed quartz, containing 99.8 per cent. pure silica, was obtained in three sizes or grades. The particles of the finest grade have an average diameter of 0.02^{mm}; those of the medium 0.6^{mm}; and those of the coarse 1.15^{mm}. To these different sands were added mineral salts which should supply the essentials for plant growth. The proportion of the ions to the volume of soil was made approximately the same as it was found to be in natural fertile soils by Taylor and Mooney.[2] The salts actually used were KH_2PO_4, $Ca(NO_3)_2$, $MgSO_4$, $NaNO_3$ and $CaCl_2$. All three grades of sand were treated exactly alike.

Three ordinary apple barrels were chosen for the cultures. These

[2] U. S. Dept. of Agric., Bureau of Soils, Bull. 22:37. 1903.

have an end diameter of 40^{cm} and a height of 70^{cm}. After a number of holes had been bored in the sides and bottom, each of these was placed upright, with the top even with the general ground surface, in gravelly sand of an ancient lake beach in the experiment grounds of this laboratory. The barrels stand in a north-and-south row about a meter apart, the finest soil being at the southern end of the row, the coarsest at the northern. Each barrel was filled to the brim with its particular grade of culture soil, the salts being added in solution as the sand was shoveled in. The soil in and around the barrels was then thoroughly soaked with water. After the

FIG. 2.

soils thus prepared had stood several days, wild plants were dug in the vicinity of the university and set out in the cultures, practically all of the soil adhering to their roots having first been removed by gentle water-washing.

Similar plants, from the same locality, and often from the same clump, were chosen for the cultures. Immediately following the planting, sufficient water to wash the soil closely around the roots was added and no subsequent watering was done. The plants used are as follows: *Poa compressa*, *Poa pratensis*, *Potentilla anserina*, *Potentilla argentea*, *Solidago serotina*, *Helianthus strumosus*, *Helianthus divaricatus*, *Verbena stricta*, and *Verbena hastata*.

Placed in the open, as the cultures are, they have been subjected to the same external moisture conditions both in regard to precipitation and

absorption from the surrounding natural soil. At the time of placing the barrels, the ground water of the ridge where they were sunk had its surface at a depth of 2.2^m, *i. e.*, 1.5^m below the bottom of the barrels. Thus the three cultures present no differences either in external water or in chemical nature, but differ only in size of their component quartz particles. It need hardly be added that the gravelly sand surrounding the barrels is perfectly uniform throughout the series.

FIG. 3.

The cultures were started May 5, 1904. For the first few days no difference was to be noted in the growth of the plants, but gradually those in the finest sand forged ahead of the others, and on June 5 a difference was very well marked. The plants in the finest material showed a much greater growth and a greater general thriftiness of vegetation. The photographs here presented exhibit clearly the relation between the three cultures as they existed on June 15. *Fig. 1* shows the condition of the culture in fine sand; *fig. 2*, that in medium sand; and *fig. 3*, that in coarse sand.

The following table shows the height in centimeters of the plants in the three cultures on June 15.

Plant	Fine soil	Medium soil	Coarse soil
Potentilla anserina	20–23	8–10	6– 8 (3 out of 4 dead)
Potentilla argentea	20–23	4– 5	3– 6
Verbena stricta	8–15	2– 5	2– 4
Verbena hastata	14–19	5– 8	2– 3
Solidago serotina	42–45	10–17	10–12
Helianthus strumosus	18–23	3–12	10–11
Helianthus divaricatus	22–28	14–19	10–17
Poa pratensis	15–20	dead	dead
Poa compressa	28–40	nearly dead	dead

While the above table is strikingly significant in showing relative size, and therefore relative rate of growth, it does not express at all the equally prominent features of comparative size and numbers of leaves, the presence or absence of runners, the wealth or scarcity of flowers, and all the features which go to make one plant vigorous and the other barely existing.

It will be realized at once that the experiment here described offers somewhat conclusive evidence in favor of the above-mentioned hypothesis of one of the present authors (*loc. cit.*), as well as of that recently expressed by Whitney and Cameron[3] in regard to agricultural plants. A fuller discussion and analysis of the conditions here dealt with would be out of place in this announcement, the purpose of the latter being only to state the facts in regard to the experiment. Further work along these lines is in progress.—Burton Edward Livingston and Gerhard H. Jensen, *The University of Chicago.*

A NEW GILIA.

Gilia sapphirina, sp. nov. (Hugelia).—Erect, paniculately branched from the base, the branches slender, sparsely leaved, the main stem and some of the principal branches inclined to be tortuous, viscid-glandular throughout, 30^{cm} high or more: leaves (all but the uppermost) simple, subterete, tipped with a white bristle, often purplish, 1–5^{cm} long; uppermost leaves with two very short bristle-tipped divisions at base: flowers solitary or capitate in few-flowered clusters from most of the leaf axils, even those near the base of the stem, either sessile or on peduncles 10–15^{mm} long; involucral bracts broadly ovate and simple or 3-lobed, membranous on each side of the broad green rib, glandular and clothed with very few woolly hairs: calyx 8^{mm} long, the divisions one-third the entire length, the central green rib 0.75^{mm} wide, slightly narrower than the membranous

[3] Whitney, M., and Cameron, F. K., The chemistry of the soil as related to crop production. U. S. Dept. of Agric., Bureau of Soils, Bull. 22:72. 1903.

fold between, glandular-puberulent and viscid, not at all lanate: corolla salverform, the tube 4^{mm} long, slightly surpassing the spine-tipped triangular divisions of the calyx; border sapphire blue, throat yellowish, lobes broadly obovate to orbicular, retuse at apex, 7^{mm} wide, 10^{mm} long; filaments and anthers white, exserted about 7^{mm}, the anthers oblong, sagittate, 3^{mm} long: style longer than the filaments but not equaling the anthers; stigmas 3 or 4, short, narrowly linear: capsule barely surpassing the calyx lobes, usually with only one seed in each cell, the other ovules present but abortive.

Type collected November 1903 by Mrs. Blanche Trask, in the San Jacinto Mountains, California. Specimen 2630 of H. M. Hall's collection from the same mountains, distributed as *G. virgata* Steud., is the same but is much younger than Mrs. Trask's specimen. Neither can be properly referred to *G. virgata* if the figure in Hooker's *Icones* 200 represents that species. The paniculate instead of virgate habit, the glandular instead of white-lanate pubescence, the distinct and broad membranous sinus of the calyx, the broad retuse lobes of the corolla, the few seeds in the capsule, all serve to distinguish them.—ALICE EASTWOOD, *California Academy of Sciences. San Francisco.*

CURRENT LITERATURE.

BOOK REVIEWS.

Alaskan cryptogams.

THE FIFTH volume of the series presenting the scientific results of the Harriman Alaskan Expedition is devoted to papers on cryptogams.[1] It has been prepared under the general direction of Dr. William Trelease, who distributed the material to specialists and writes an interesting introduction to the volume. Dr. Trelease also shares with P. A. Saccardo and C. H. Peck in the section on fungi; the lichens are treated by Miss Clara E. Cummings, with admirably simple keys; the algae by DeAlton Saunders; mosses by J. Cardot and I. Thériot; sphagnums by C. Warnstorf, whose determinations have been edited by Trelease; the liverworts by A. W. Evans; and the pteridophytes by William Trelease.

Three of these papers, those on algae, mosses, liverworts, have already been printed in the *Proceedings* of the Washington Academy of Sciences. In this volume they are reprinted from the same electrotype plates, even to typographical errors. The utmost care has been taken to preserve the original pagination and plate numbers, so that from this volume the original publication may be quoted—a bibliographical precaution which deserves thankful recognition. It would be impossible to praise too highly the typographical elegance and beauty of this volume. No detail has been overlooked. Paper, letter-press, plates, and binding combine to make it an example of the best work of American book-makers.

And the contents, judging by the reputation of the authors of the various papers, is worthy of the perfect dress. About 75 species and 35 subspecies and varieties are described as new. Many are illustrated upon the 44 plates, of which those for fungi are colored. The clever and artistic head pieces were designed by Mr. F. A. Walpole, whose recent untimely death robs the Department of Agriculture of its most skilful botanical artist.

The phanerogams are to be presented in two volumes, under the editorship of Mr. F. V. Coville, which are announced for the present year.

Mr. Harriman deserves the cordial thanks of naturalists, not only for the expedition itself which extended so much the knowledge of the Alaskan region, but also for the sumptuous style in which he makes it possible for the results to be presented.—C. R. B.

[1] J. CARDOT, CLARA E. CUMMINGS, ALEXANDER W. EVANS, C. H. PECK, P. A. SACCARDO, DEALTON SAUNDERS, I. THÉRIOT, AND WILLIAM TRELEASE, Alaska. Vol. V. Cryptogamic botany. Harriman Alaska Expedition. With cooperation of Washington Academy of Sciences. Imp 8vo. pp. x+424. *pls.* 43. New York: Doubleday, Page & Co. 1904. $5.00.

NOTES FOR STUDENTS.

KOERNICKE finds that Roentgen rays, after first accelerating growth for a brief period, as do many injurious agents, later retard it.[2] Experiments with radium bromid[3] inclosed in glass, so that only the β and γ rays acted (α rays and the gaseous emanation being stopped by the glass), showed a strong retardation of the growth of seedlings, but no fatal injury. Somewhat similar inhibition of growth occurred with certain fungi after prolonged action of the rays.—C. R. B.

HARVEY[4] has made a study of the physiographic ecology of Mount Ktaadn, tracing the origin and development of the flora and noting the various factors operative in determining the present plant physiognomy. He also shows that the accepted principles of physiographic ecology hold in general in alpine as well as in lowland regions. The associations discussed are the crustaceous lichens, the reindeer moss, the alpine-tundra, the "Krummholz," the Picea-Abies forest, the "roches moutonnées," the pioneer stage of the alpestrine meadows, the meadow stage, the shrub stage, ponds, and sphagnum bogs.—J. M. C.

BOODLE[5] has made an experimental study of the ecological anatomy of the leaves of Pteris. Leaves grown in dry and exposed situations are xerophytic and have a "hypoderm;" while those sheltered and shaded are of the "shade-leaf" type, having no hypoderm and either weakly developed or no palisade tissue. The same differences were developed by different leaves of the same plant, and by different parts of the same leaf. A plant grown first in a damp greenhouse and then in the garden produced shade-leaves in the former and sun-leaves in the latter. It was further noted that the mature type of structure is not determined at an early stage in the growth of the leaf.—J. M. C.

SEWARD[6] considers the Carboniferous, Rhaetic, and Wealden floras of South Africa in an important paper. The Ecca beds are held to correspond in a general way with the Upper Carboniferous of the northern hemisphere, and are more definitely correlated with the Karharbári beds of the Lower Gondwana in India. Evidence from the contained plants emphasizes the well-known similarity which existed during the Carboniferous between the floras of India, South

[2] KOERNICKE, MAX, Ueber die Wirkung von Röntgenstrahlen auf die Keimung und das Wachsthum. Ber. Deutsch. Bot. Gesells. **22**:148–155. 1904.

[3] KOERNICKE, MAX, Die Wirkung der Radiumstrahlen auf die Keimung und das Wachsthum. *ibid.* 155–166. *pl. 10.* 1904.

[4] HARVEY, LE ROY HARRIS, A study of the physiographic ecology of Mount Ktaadn, Maine. The University of Maine Studies, no. 5. pp. 50. *figs. 6.* Dec. 1903.

[5] BOODLE, L. A., The structure of the leaves of the bracken (*Pteris aquilina* Linn.). Jour. Linn. Soc. Bot. **35**:659–669 1904.

[6] SEWARD, A. C., Fossil floras of Cape Colony. Ann. S. African Museum **4**: 1–116. *pls. 14. figs. 8.* 1903.

Africa, and South America. The Stormberg beds are considered as of Rhaetic age, and four new species are described. The Uitenhage beds are considered as probably of Wealden age, and the fragmentary remains of nineteen species of plants are enumerated, of which two, a Nilssonia and an Araucarites, are described as new.—EDWARD W. BERRY.

REED[7] has made a cytological study of enzyme-secreting cells in corn and date seedlings. Sections of living tissue were compared with fixed material to avoid error. Torrey's technique[8] is regarded faulty, and no evidence was found to support his observation that solid matter extrudes from the nucleus through interruptions of the nuclear membrane into the cytoplasm. In addition to a careful study of the literature and some valuable data in technique, the observations of special interest are: "(1) In the resting condition the secreting cells of both Zea and Phoenix are crowded with relatively small proteid granules. As secretion begins these granules gradually disappear. In Zea this disappearance coincides closely with consumption of the endosperm; in Phoenix, however, the granules disappear long before the endosperm is dissolved. (2) The chromatin of the nucleus is small in amount at the beginning of secretion and increases as germination progresses. These changes are more noticeable in the case of Zea than in Phoenix."—RAYMOND H. POND.

WIELAND[9] has brought together a large array of facts to support the thesis that polar climate has been the major factor in the evolution of plants and animals. He shows that climatic changes of a character affecting life must in the course of time be at a minimum at the equator and at a maximum at the poles. He also thinks it reasonable that the origin of life itself took place at the north or at both poles; and that the Palaeozoic for various reasons was a period mainly of "generalized origins." From the origin of life down to the Mesozoic the north and south polar areas may have played a well-nigh equal part in creating a certain southward and northward stress; but beginning with the Mesozoic and "extending to the glacial period, overwhelming evidence points to the polar origin and continuous outward dispersion from the north polar area of most of the great plant and vertebrate groups." Among the illustrations of this the author calls attention to "the outward movement especially of conifers and dicotyls from the Arctic area for long periods of time."—J. M. C.

WAGER,[10] in a preliminary paper, has discussed the much debated question of the cell structure of the Cyanophyceae. He concludes that the central body

[7] REED, H. S., A study of the enzyme-secreting cells in the seedlings of *Zea Mais* and *Phoenix dactylifera*. Annals of Botany **18**:267. 1904.

[8] TORREY, Cytological changes accompanying the secretion of diastase. Bull. Torr. Bot. Club **29**:421. 1902.

[9] WIELAND, G. R., Polar climate in time the major factor in the evolution of plants and animals. Am. Jour. Sci. IV. **16**:401–430. 1903.

[10] WAGER, HAROLD, The cell structure of the Cyanophyceae. Preliminary paper. Proc. Roy. Soc. **72**:401–408. 1904.

is a nucleus of a "simple or rudimentary type," although not to be regarded as one of normal type, similar to the nuclei of the higher plants. He enumerates twelve main chemical and morphological characters that belong to the nuclei of higher plants, and claims that at least seven of them belong to the central body of the Cyanophyceae, as follows: (1) presence of a nuclear network, (2) reaction to nuclear stains, (3) behavior toward digestive fluids, (4) presence of phosphorus, (5) presence of masked iron, (6) amitotic division, and (7) presence of chromatin granules on a linin framework. It differs from the nuclei of higher plants in the absence of a true mitosis with spindle fibers, and in the absence of a nuclear membrane and a nucleolus, although in certain conditions both membrane and nucleolus are said to be suggested. The author evidently regards this central body as a developmental stage in the evolution of the nucleus of higher plants.—J. M. C.

BECAUSE of their perishable nature fungi are rare as fossils, and yet Weiss[11] finds the remains of a parasitic fungus on stigmarian rootlets from the Lower Coal Measures. Magnus has compared this type with the existing Urophlyctis, which it resembles not only in so much of its structure as is discernible, but also in its similar habit of growing on plants which inhabit marshy or at least wet situations. Weiss accords in this identification to the extent of naming the fossil *Urophlyctites Stigmariae*.

The same author[12] notes a mycorhiza from the same geological horizon. Janse is quoted as saying that 69 out of 75 plants in a tropical forest have their roots infested by symbiotic fungi, and while this condition argues considerable specialization on the part of both, the similar conditions that prevailed during the Carboniferous mitigates our surprise at finding symbiosis occurring so far back as this. The roots have not been associated with the plant which bore them; they are possibly lycopodiaceous and are referred to the form-genus Rhizonium of Corda. The hyphae are for the most part intracellular, but in no case is there any sign of injury to the host. The fungus is named *Mycorhizonium*, and is considered as possibly belonging to the Phycomycetes.

ZODDA[13] records the finding of a cone of a species of Pinus still living, in the Lower Pliocene of Sicily.—EDWARD W. BERRY.

A HYBRID between *Drosera rotundifolia* and *D. longifolia* was investigated about a year ago by Rosenberg.[14] He found that *D. rotundifolia* has ten chromosomes in the pollen mother-cells, while *D. longifolia* has twenty; further, that in the hybrid there are found pollen mother-cells with ten, twenty, and

[11] WEISS, F. E., A probable parasite of stigmarian rootlets, New Phyt. **3**:63–68. 1904.

[12] WEISS, F. E., A mycorhiza from the Lower Coal Measures. Annals of Botany **18**:255–265. *pls. 18, 19.* 1904.

[13] ZODDA, G., *Pinus Pinea* L. fossile nel Pontico di Messina. Malpighia **17**: 488–492. 1903.

[14] Review in BOT. GAZ. **36**:152. 1903.

fifteen chromosomes, the ten and twenty being the number characteristic of pure pollen mother-cells of the two parents, while the number fifteen is just what one would expect in the pollen mother-cells of a genuine hybrid. A recent paper[15] records the results of investigations upon the embryo sac mother-cells of the parent and the hybrid. The sporophytic cells of the hybrid always show thirty chromosomes. In the pollen mother-cells and embryo sac mother-cells, the number of chromosomes is twenty, a very surprising number. These twenty chromosomes are not alike, but of two sizes, ten being large and ten small. The large chromosomes are evidently double and the small ones single. *D. rotundifolia* is represented in the hybrid by ten chromosomes and *D. longifolia* by twenty. In the mother-cell the ten chromosomes of *D. rotundifolia* fuse with ten of *D. longifolia*, thus leaving the other ten chromosomes of *D. longifolia* single. These are the numbers as seen during the metaphase. The daughter nuclei of the tetrads contain quite regularly ten chromosomes, presumably five being single and five double. It is evident that these observations have an important bearing upon the problem of the reduction of chromosomes, and it is to be hoped that the full account of the investigations will not be long delayed.—C. J. CHAMBERLAIN.

WITH THE rediscovery of Mendel's laws by Correns, Tschermak, and De Vries, there has been a revival of interest in the fundamental problems of heredity and hybridization, and many works of both experimental and speculative character have appeared. One of the most active workers in this field is Correns. In several recent papers he has presented an account of some of his hybridizing experiments and has discussed questions of dominance.

A very striking result of experiments with Mirabilis hybrids[16] was the production of characters in the offspring, which were found in neither parent. Thus the offspring of dark yellow or pale yellow *Mirabilis Jalapa* crossed with the pure white form, never showed either yellow or white, but all were red or rose-colored. In the second generation these red-flowered hybrids gave rise to a whole series of forms, red-striped, white, pale yellow, rose, and red. Similarly *M. Jalapa* of whatever color crossed with *M. longiflora* (white with a red-violet throat), resulted in offspring having violet corollas, differing in the different cases only in the intensity of the color.

In discussing dominance[17] he points out that there may be every degree of dominance and suggests that a character be considered dominant if it occur in 75 to 100 per cent. of the offspring, and recessive if it occur in 0 to 25 per cent. of the offspring. Characters transmitted to 25 to 75 per cent. are intermediate;

[15] ROSENBERG, O., Ueber die Tetradenteilung eines Drosera-Bastardes. Ber. Deutsch. Bot. Gesells. **22**:47–53. *pl. 4.* 1904.

[16] CORRENS, C., Ueber Bastardirungsversuche mit Mirabilis-Sippen. Ber. Deutsch. Bot. Gesells. **20**:594–608. 1902.

[17] CORRENS, C., Ueber die dominierenden Merkmale der Bastarde. Ber. Deutsch. Bot. Gesells. **21**:133–147. 1903.

there is no dominance. Careful determinations of the intensity of color in parents and offspring showed that many errors have been made regarding dominance, through the neglect of Weber's law. The intensity of the color does not measure the amount of pigmentation. He concludes that complete dominance is much less common than has been supposed. In a second paper on dominance[18] he presents a number of cases which do show complete dominance; *e. g.*, *Hyoscyamus annuus*×*niger* shows absolute dominance of the biennal habit. Rimpau found, on the other hand, that the annual habit is completely dominant in *Beta patula* × *vulgaris;* dioecism dominates monoecism in *Bryonia alba*×*dioica*. Correns opposes the statement by De Vries that dominance is characteristic of hybrids between races and that hybrids between species are intermediate. He shows that in form and color of root the hybrids between turnip races are intermediate, and he also gives examples of dominance in hybrids between distinct species. He discusses[19] the unique suggestion of De Vries that hybrids which fail to "split" in the second generation have *Anlagen* in one parent unmatched by corresponding *Anlagen* in the other, and concludes that no such condition exists, and that if no splitting occurs it is due to some other cause than that there is nothing to split.

Correns has recently reviewed[20] the present state of our knowledge of the origin of species. He presents the experimental work which has been done, laying most stress on the work of De Vries and Johannsen. The presentation is fair in the main, but one cannot avoid feeling that he begs the question as to the significance of individual variations for evolution, when he distinguishes mutations as *inheritable* variations, however slight.—G. H. SHULL.

[18] CORRENS, C. Weitere Beiträge zur Kenntnis der dominierenden Merkmale und der Mosaikbildung der Bastarde. Ber. Deutsch. Bot. Gesells. **21**:95–201. 1903.

[19] CORRENS, C., Die Merkmalspaare beim Studium der Bastarde. Ber. Deutsch. Bot. Gesells. **21**:202–210. 1903.

[20] CORRENS, C., Experimentelle Untersuchungen über die Entstehung der Arten auf botanischen Gebiet. Arch. f. Rassen- und Gesellschafts-Biologie **1**:27–52. 1904.

NEWS.

W. A. MURRILL has succeeded F. S. Earle at the New York Botanical Garden as assistant curator in charge of the fungi.

PROFESSOR F. L. STEVENS has been elected president of the North Carolina Academy of Science for the ensuing year.

COLUMBIA UNIVERSITY has recently conferred the honorary degree of Sc.D. upon Professor Hugo DeVries, of Amsterdam.

EDWARD W. BERRY has been elected secretary of the Torrey Botanical Club in the place of Professor F. S. Earle, who recently left for Cuba.

THE UNIVERSITY OF WISCONSIN at its recent Jubilee conferred the honorary degree of LL.D. upon Professor W. G. Farlow, of Harvard University.

D. T. MACDOUGAL, director of the laboratories of the New York Botanical Garden, has been advanced to the position of assistant director of the institution.

DR. C. C. HOSSEUS left Berlin on June 22 for a collecting expedition in Siam. The sets of plants obtained will be sold from the Royal Botanic Museum of Berlin.

A. F. BLAKESLEE of Harvard University has received a grant from the Carnegie Institution to spend next year in Europe continuing his mycological investigations.

JOHN MACOUN, the veteran botanist of the Canadian Geological Survey, will spend this summer in the Rocky Mountains of Canada making extensive collections of cryptogams.

AT THE RECENT annual meeting of the Linnean Society (London) the supplemental charter was laid before the fellows, one item of which gives authority to elect women to membership.

LAETITIA MORRIS SNOW received the degree Ph.D. at the June convocation of the University of Chicago, the subject of her thesis being "The effect of external agents upon the development of root hairs."

MEL T. COOK, formerly in charge of botany at DePauw University (Greencastle, Indiana), has been appointed plant pathologist at the Experiment Station of Cuba, newly established at Santiago de las Vegas.

THE UNIVERSITY OF GÖTTINGEN has awarded its Otto Wahlbruch prize, of the value of $3000, to Dr. Wilhelm Pfeffer, professor of botany at Leipzig. The prize is awarded for the most prominent contribution to science during the past two years.—*Science*.

MR. L. B. ELLIOTT, editor of the *Journal of Applied Microscopy* since its beginning in 1898, has severed his connection with the Bausch & Lomb Optical

Company to accept another position. He will continue his private work in laboratory photography and biology as heretofore, his address being 17 Birr Street, Rochester, N. Y.

DR. F. L. STEVENS has been promoted to the professorship of botany and vegetable pathology in the North Carolina College of Agriculture and Mechanic Arts. A new building is about to be constructed which will provide a well-equipped bacteriological laboratory, a plant-disease laboratory, and an elementary laboratory, together with offices for the professor and assistants, research rooms, and greenhouses for experimental work.

THE ANNUAL REPORT of the Secretary of the Botanical Society of America embodied in Publication 24 is a statement of conditions and record of progress during the first decade of the existence of the Society. The total constituency of the Society now numbers 58, and its accrued funds amount to nearly three thousand dollars, a large part of which is treated as permanent endowment, the income only being used. Recently the policy was adopted of making grants from current funds in aid of investigations by members and associates. Thus far grants to the amount of $840 have been made.

In order to promote unity of botanical interests a committee consisting of B. T. Galloway (chairman), C. R. Barnes, and C. E. Bessey has been appointed and requested to prepare a plan for cooperation with other botanical organizations, for consideration at the eleventh annual meeting.

The increasing demand upon the time allowed by the Society for the presentation of scientific papers has made necessary the action of the Council in accepting only papers from members, associates, and persons specially invited by the Council to contribute.

THE MANAGERS OF the Louisiana Purchase Exposition have arranged for an International Congress of Arts and Sciences, to be held in the Exposition grounds September 19–25. W. G. FARLOW, Harvard University, will preside over the general section of *Biology*, before which the speakers will be JACQUES LOEB, University of California, and JOHN M. COULTER, University of Chicago. HUGO DE VRIES, University of Amsterdam, will be one of the speakers before the subsection of *Phylogeny*. For the strictly botanical sub-sections the following appointments have been made. *Plant Morphology:* chairman, WILLIAM TRELEASE, Washington University, St. Louis; speakers, FREDERICK O. BOWER, University of Glasgow, and KARL F. GOEBEL, University of Munich; *Plant Pathology:* chairman, CHARLES R. BARNES, University of Chicago; speakers, JULIUS WIESNER, University of Vienna, and BENJAMIN M. DUGGAR, University of Missouri. *Plant Pathology:* chairman, CHARLES E. BESSEY, University of Nebraska; speakers, JOSEPH C. ARTHUR, Purdue University, and another to be selected. *Ecology:* chairman, CONWAY MACMILLAN, University of Minnesota; speakers, OSKAR DRUDE, Königl-Technische Hochschule, Dresden, and CHARLES FLAHAULT, Director of the Botanic Institute, Montpellier, France. *Bacteriology:* chairman, HAROLD C. ERNST, Harvard University; speakers, EDWIN O. JORDAN, University of Chicago, and THEOBALD SMITH, Harvard University.

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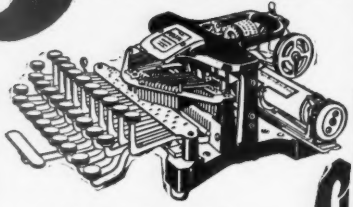

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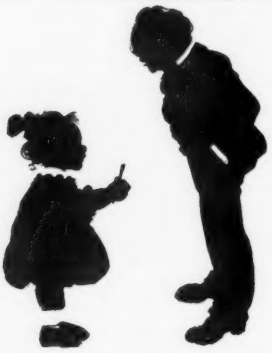

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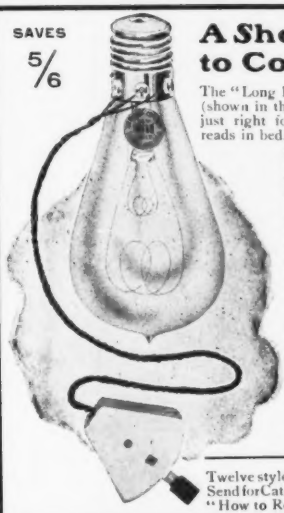

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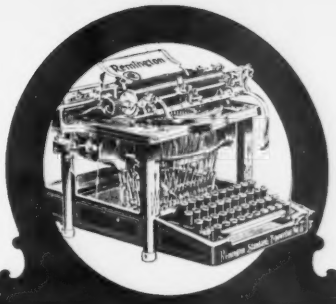

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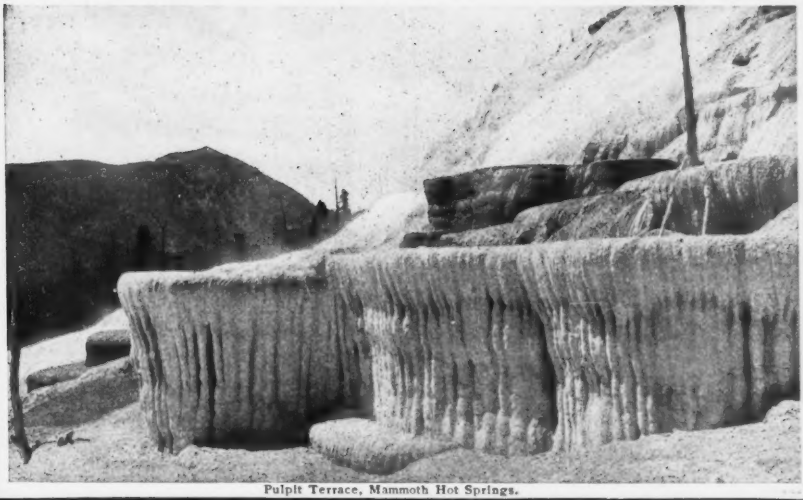

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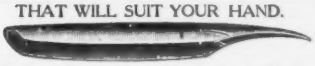

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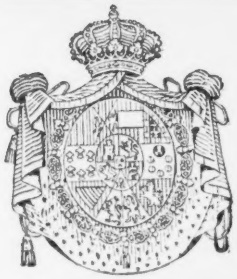

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